VOLUME XXXVI NUMBER 2

BOTANICAL GAZETTE

AUGUST, 1903

STUDIES IN SPINDLE FORMATION.

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(WITH PLATES XV AND XVI)

HISTORICAL.

THE evidence produced from the researches of the last few years[1] proves quite conclusively that a centrosome as a spindle-forming organ does not exist in the higher plants. Too few forms, however, have been worked out in sufficient detail to allow of any definite conclusions as to whether or not these plants have any common uniform method of spindle formation. Of the types that have been thoroughly examined, the following have been recorded:

In 1897 Osterhout investigated the spindle in the spore mother-cells of Equisetum. The first indication of a spindle in these cells is the formation of a felted zone of kinoplasmic fibers surrounding the nucleus. These fibers grow out from the nuclear membrane and assume a radial position. By the fusion of their free ends these fibers form a series of cones, and upon the breaking down of the nuclear membrane the cones unite at their apices in two groups to form the bipolar spindle.

In 1898 the writer investigated the development of the spindle in the pollen mother-cells of Cobaea. Here it was found that, as division approaches, a dense granular cytoplasmic substance

[1] Belajeff (1894), Byxbee (1900), Davis (1899, 1901), Debski (1897), Farmer (1893, 1895), Guignard (1898), Juel (1897), Lawson (1898, 1900), Mottier (1897 *a*, *b*,) Němec (1898, 1899), Osterhout (1897, 1902), Smith (1900), Strasburger (1896, 1897, 1900), Webber (1897), Weigand (1899), Williams (1899).

forms a complete zone about the nucleus. The nuclear wall disappears, and the central part of the cell becomes filled with a network of kinoplasmic fibrils, in which the chromosomes lie. This network grows out into several projections, which become the primary cones of the multipolar spindle. These cones now unite at their apices into two groups and thus form the bipolar spindle.

In 1899 Williams describes for Passiflora a process somewhat resembling that which occurs in Cobaea. Upon the breaking down of the nuclear wall, there is a large kinoplasmic network formed in the central portion of the cell. This network of fibrils projects outward at various points and becomes cones, which, uniting at their apices in two groups, form the mature spindle.

In 1900 the writer investigated the spindle in Gladiolus. Here, as in Equisetum, the first indication of the spindle in the mother-cell is the formation of a felted zone of kinoplasmic fibrils surrounding the nucleus. But instead of the fibrils taking on a radial arrangement, as described for Equisetum, the zone grows out at irregular intervals in the form of sharp pointed projections, which are the primary cones of the spindle. The nuclear wall remains intact until the cones are fully developed, and upon its breaking down the cones collect by the fusion of their apices into two groups, when the bipolar condition is reached.

Byxbee (1900) has recorded the following method for the development of the spindle in the pollen mother-cells of Lavatera. The meshes of the network close to the nuclear wall pull out in a direction parallel to the wall, forming a felt of fibrils about the nucleus. The cytoplasm now collects in a dense granular zone about the nuclear membrane, as it does in Cobaea. Upon the breaking down of the nuclear wall, there is formed a central mass of fibrils in which the chromosomes are suspended. This central mass of fibrils grows out into several projections, bringing about the multipolar condition of the spindle. Two of the cones become more prominent than the others, which they absorb, and the bipolar figure is thus produced.

Smith (1900) has worked out with considerable detail the

development of the spindle in the spore mother-cells of Osmunda. In this case the spindle originates from a zone of kinoplasm which surrounds the nucleus. The granules in the kinoplasm arrange themselves in rows, concentric with the nuclear wall, and are finally massed on opposite sides of the nucleus. From these masses two cones of fibrils are developed, which become the two cones of the spindle. As there are only two primary cones developed, the spindle is bipolar from the first.

Osterhout (1902), in his recent work on Agave, records the following series of events leading to the formation of the spindle in the mother-cell. During the early stages there is developed a cytoplasmic membrane outside of the nuclear wall. This he calls the "spindle membrane," and he regarded it as a unique structure. There is no weft of fibrils formed, but the spindle-forming fibrils are radial from the beginning, and are attached to both the nuclear and spindle membranes. From these radial fibrils the cones are developed, and these, by fusing into two groups, bring about the bipolar condition. Probably the most remarkable observation that Osterhout has recorded is that the second spindle formation differs entirely from the first. According to his observations, the spindle-forming fibrils of the second division are found in close contact with the nuclear wall, and their free ends radiate from it. They extend outward into the cytoplasm, and by the union of their ends form a series of cones. These fuse at their apices into two groups and form the bipolar spindle in much the same fashion as in Equisetum.

From the observations of the writers described above it is perfectly obvious that there are considerable differences between the methods of spindle formation. It is also evident that there are certain important features which are common to nearly all of them. It would seem that there are several distinct types of spindle formation, but the differences between them are too great, and the number of forms worked out in detail are too few to allow of any generalizations. The number and character of these types can be determined only by additional observations. It is to this end that the following studies are recorded.

METHODS.

These were essentially the same as those used in my work on Cobaea and Gladiolus. As full details are recorded in these papers, it will be unnecessary to repeat them. It is only necessary to add that the material was all fixed in the field, and by far the most satisfactory results were obtained by using Flemming's weak solution of chromic-osmic-acetic acid as a killing agent, and the triple stain, safranin, gentian, and orange G.

THE POLLEN MOTHER-CELLS OF IRIS FLORENTINA.

The young anthers of the common garden Iris furnish very good material for the study of spindle formation. If conditions are favorable and the material is fixed in the field, immediately after being detached from the plant, all the stages in the formation of the spindle of the first division of the pollen mother-cells may be observed in a single anther. As the anthers at this stage are very large, many sections may be obtained from one of them. Previous to the formation of the first spindle, the nucleus of the mother-cell is very large, containing one or two nucleoli and the chromatin thread. The cytoplasm appears to be a reticulum, the threads of which are more or less granular. In the immediate neighborhood of the nuclear wall, the cytoplasm is more dense than at the periphery, but this dense region is not as sharply differentiated as that described by the writer for this stage in the pollen mother-cells of Cobaea and Gladiolus. Numerous small spherical bodies, probably oil globules, were found distributed irregularly through the cytoplasm.

While the chromatin is yet in the spirem stage, the cytoplasm immediately in contact with nuclear membrane becomes differentiated into a distinct weft or felted zone of fibrils. This weft appears at first to consist of a few delicate but very distinct fibrils, which stain blue with the gentian violet, in contrast to the slightly orange color of the rest of the cytoplasm. They do not radiate from the nuclear membrane, but lie more or less parallel to it. When followed along their course, they were found to lose gradually their affinity for gentian violet, and to terminate in the regular orange-colored threads of the cytoplasm. This indicates

that the kinoplasmic threads are nothing more than modified threads of cytoplasm, which have lost their reticulated and granular character and have become more distinctly thread-like. *Fig. 1* shows one of the early stages in the formation of the weft, which ultimately develops into the spindle. Even in stages earlier than this, the fibrils were sharply differentiated, both in their structure and staining properties, from the surrounding cytoplasm. The fibrils gradually increase in numbers, evidently at the expense of the reticulum of the cytoplasm, and soon a fibrous zone of considerable thickness completely surrounds the nuclear membrane *fig. 2*. As far as the development of this zone is concerned, the process is identical with that which occurs in Gladiolus (Lawson, 1900). In Gladiolus, however, the chromosomes were already formed when the weft was developing, while in Iris the chromatin is yet in the spirem stage.

Fig. 2 shows the appearance of the fibrous zone when fully developed. Up to this time it increased in thickness almost uniformly, but it now grows outward at irregular intervals. Two of these outward projections are shown in *fig. 2*. The meshes formed by the interlacing fibrils of the weft become elongated in the directions in which the fibrils are growing, that is, in the direction of the projection. These outgrowths of the fibrous zone are the first indications of the primary cones of the so-called multipolar stage of the spindle, and the threads composing them converge toward their apices.

During the development of the cones the chromatin assumes the form of distinct chromosomes, and the nucleoli become vacuolated.

The development of the cones is not only brought about by the pushing out of the original weft at certain intervals, but they apparently increase at the expense of the cytoplasm into which they project. *Fig. 3* shows one of the cones projecting into the cytoplasm, and the outermost fibrils converging to its apex are continuous with the fibrils of the cytoplasmic reticulum. *Fig. 4* shows the cones at a later stage; the larger cone is much more sharply defined. It has lost much of its reticulated appearance, and its fibrils are more independent of one another, except

where they converge at the apex. There is apparently no definite position for the projection of each cone. They may be separated by considerable distance, or again there may be two or three quite close together (*figs. 5, 6*). The number also seems to vary, although there are always more than two formed. Cross sections always show three or four. *Fig. 6* shows three on one side, and an indication of a fourth on the opposite side of the nucleus. This figure also shows that the growth of the various cones is not simultaneous.

One of the striking features of the cones is the remarkably sharp point with which each one terminates. These sharp-pointed apices extend outward as the fibrils composing the cones elongate, and they indicate the outermost points at which are taking place the changes which bring about the transformation of the cytoplasmic reticulum into spindle-forming fibrils.

As in Gladiolus, the nuclear membrane persists until the cones have almost attained their maximum development. In *fig. 7* a portion of the nuclear wall remains, and several of the cones have fused together before the nuclear membrane entirely disappears. This fusion, however, probably does not begin until the nuclear wall begins to break down. When this is accomplished the chromosomes become attached to the fibrils at the base of the cones. During and after this stage the collecting together of the cones was very noticeable.

By the time the nuclear wall has entirely disappeared, and all the chromosomes are connected with the fibrils, the cones unite at their apices into several groups (*fig. 8*). Here three of these groups are represented, which are the product of the union of several primary cones. The space that was occupied by the nuclear sap is now filled with a complex of delicate fibrils, and all of the chromosomes are connected with fibrils which extend to the apex of one or other of the cones. By further union of the cones (*figs. 9, 10*), the number of cone aggregates is reduced to two. Up to and including the stage represented in *fig. 9*, the fibrils composing the cones were of the same general character, but in the following stages there is a differentiation of the fibrils, according to the part they take in the mature spindle. We have,

for instance, those that are connected with the chromosomes, those that extend from end to end of the spindle, and those that extend laterally outward with their free ends projecting into the cytoplasm. These are known as the connective, continuous, and mantle fibers respectively.

The spindle having now reached the bipolar condition, and the connective fibrils from the respective poles having become connected with the chromosomes (*figs. 10, 11*), the latter bodies take up their characteristic position at the equator, and the formation of the spindle is complete.

The series of events leading to the formation of the spindle, as here described for Iris, agrees in every essential detail with those which occur in Gladiolus.

THE POLLEN MOTHER-CELLS OF DISPORUM HOOKERI.

The anthers and pollen mother-cells of Disporum are not as large as many other liliaceous types that have been used for the study of spindle formation ; nevertheless, they form an extremely interesting subject. When properly fixed in the field, the various stages in the formation of the first spindle of the mother-cell may be readily obtained.

In the resting condition of the mother-cell, the nucleus is centrally situated, but as division approaches it is invariably found near one side. Before any kinoplasmic differentiation takes place, the chromatin has broken up and assumed the form of definite spherical chromosomes, of which there are but eight. The first evidence of spindle formation is to be found in the transformation of the cytoplasm in the immediate vicinity of the nuclear membrane. At first, this change takes place in much the same manner as described above for Iris. There are in the beginning but a few short threads, which when followed outward are found to be continuous with the reticulum of the surrounding cytoplasm, but they have lost the granular character and stain blue with the gentian violet. These threads increase in number and gradually form a distinct weft, which appears to form more abundantly on one side of the nucleus than on the other; that is, it is much more evident on the side

of the nucleus farthest away from the cell wall (*fig. 12*). While the beginning of the weft resembles that described for the stage in Iris, it soon takes on a very different form as it increases in size. Instead of the meshes running more or less parallel to the membrane of the nucleus, they elongate more at right angles to it (*figs. 12, 13*). The fibrils composing the weft stain deep blue, while the peripheral cytoplasm stains slightly orange. If, however, we follow the individual fibrils outward, they gradually lose their property of staining blue and stain slightly orange. They are, in fact, strictly continuous with the more granular threads of the cytoplasmic reticulum. They therefore seem to be nothing more than transformed threads of cytoplasm.

As already stated, the growth of the weft is not uniform; it is much more conspicuous on one side of the nucleus than on the other. This irregularity is carried still farther as the weft increases in size. The meshes elongate much more, the individual fibrils which form them lengthen considerably, and their individuality becomes much more pronounced. As the weft now increases, it does so by several projections, which terminate in sharp points, so that we have distinct cones formed (*fig. 14*), in much the same manner as they are formed in Iris. These cones at first vary considerably in number and size, and are invariably much more numerous on the side of the nucleus away from the cell wall (*fig. 14*). From a careful study of the development of these cones as they project into the cytoplasm, there seems to be little doubt that the fibrils composing them are transformed directly out of the reticulum of the cytoplasm. This is particularly evident in the earlier stages, where there is no sharp differentiation between the ends of the fibrils of the weft and the surrounding threads of cytoplasm, the one passing into and apparently being continuous with the other.

As the cones project outward, they terminate in very sharp points and extend over half way to the cell wall opposite (*figs. 14, 15*). During the entire process of their development the nuclear membrane and the nucleolus persist. There is no evidence of the breaking down of these structures until the cones are fully developed. As soon as the cones cease growing out-

ward, the nuclear membrane disappears rapidly, and the ends of the fibrils at the base of the cones become attached to the chromosomes.

The sequence of events which leads to the bipolar condition of the spindle is essentially the same as that described for Iris. Upon the breaking down of the nuclear membrane the apices of certain of the cones move toward each other and form several groups of cones. These in turn unite still further, until we have the characteristic so-called multipolar spindle. *Fig. 16* shows a stage approaching the bipolar condition. The connective fibers which attach themselves to the chromosomes become more sharply defined than the other fibrils, and appear to be thicker in the region of the chromosomes, as if they had already begun to contract. By the time the chromosomes have arranged themselves at the equatorial plate, the cones have united into two groups, which are the poles of the bipolar spindle. The mature spindle does not show the free mantle fibers which are so characteristic of Cobaea, Gladiolus, Iris, and many other forms. There are a few delicate continuous fibrils, which extend from pole to pole. The connective fibrils are much coarser than the continuous ones, stain more deeply, and are much more clearly defined. In the bipolar stage of the spindle, these fibrils appear to be much thicker in the region of the chromosomes, which suggests that they have not begun to contract, but that the chromosomes imparted the stimulus to contract. This condition of the fibrils is shown in *fig. 17*.

As the chromosomes (eight in polar view) approach the poles, the connective fibrils shorten and thicken, and by the time they have reached the poles the connective fibrils have disappeared entirely; the continuous fibrils, however, have increased in numbers. Having reached the poles, the chromosomes unite and form a mass of chromatin at each end of the spindle. Nuclear sap is now secreted, and a membrane is formed about each daughter nucleus.

The daughter nuclei are small, and the various stages in the development of the spindle of the second division were difficult to follow. The early weft stage, however, was observed, as well

as the later multipolar stages, which show clearly that the process of spindle formation in the second division is essentially the same as in the first.

THE POLLEN MOTHER-CELLS OF HESPERALOE DAVYI.

As in Iris and Disporum, the first indication of spindle formation in the pollen mother-cells in Hesperaloe is the differentiation of the cytoplasm in the immediate neighborhood of the nuclear wall into a distinct weft of fibrils. This weft is very small at first, but as it stains blue very readily when the triple stain is used, it can be clearly distinguished. The fibrils run almost parallel with the nuclear membrane, even at the beginning of their formation, and they keep this position until the weft has reached a considerable thickness. In this respect it is almost identical with Gladiolus and Iris, but differs slightly from Disporum. *Fig. 18* shows the weft fairly well developed. It encreases uniformly and completely surrounds the nuclear membrane. As in Iris and in Disporum, there is no sharp differentiation between the outer fibrils and the reticulum of the surrounding cytoplasm. It would seem that the cytoplasm loses its granular structure, becoming more distinctly threadlike, with meshes parallel to the nuclear wall, and stains blue instead of orange.

Following the same series of events that occur in Gladiolus, Iris, and Disporum, the weft soon ceases its uniform growth and proceeds to grow out at irregular intervals in the form of pointed projections. The meshes of the weft in these outward growths are no longer parallel to the nuclear membrane, but are elongated in the direction of the projections. *Fig. 19* shows one of these projections. It also shows that the fibrils of the developing cone pass into the threads of the surrounding cytoplasmic reticulum, suggesting that they grow at the expense of the cytoplasm. As the cone pushes outward, the meshes elongate proportionately, and the fibrils composing them become much more sharply defined. As in Iris and Disporum, there appears to be no definite number of cones formed; there are usually four or five to be seen in section.

As the apices of the cones approach near to the cell wall, the nuclear membrane breaks down, and the space once occupied by the nuclear sap becomes filled with the ingrowing fibers of the base of the cones (*fig. 20*). By the time the nuclear wall has disappeared, some of the cones unite at their apices. This union continues in the same fashion as that described in Gladiolus, Iris, and Disporum. *Fig. 21* shows a condition in which the nuclear wall has entirely disappeared, and five cones are seen in section. Some of these cones are evidently the result of the union of several primary cones. By the time this stage is reached the fibrils have become long independent threads, converging to the apices of the cones, and many of them have become attached to the chromosomes.

The fusion of the cones is probably a very rapid process, as the multipolar stages were only obtained from material fixed in the field, immediately after being dissected from the plant. They are never found as frequently as the bipolar stage.

Fig. 22 shows the cones uniting into two groups, pointing in opposite directions. Before fusing, the cones point outward in all directions, so that in a section few of them show (*fig. 21*), but as they collect in groups a median section shows many more in the same plane. When the bipolar condition is finally reached, the usual three sets of fibrils are sharply differentiated. The connective fibrils are clearly defined and appear to be thicker in the region of the chromosomes. The continuous fibrils extend uninterruptedly from pole to pole and are much finer than the connective fibrils. Extending laterally from the poles, numerous mantle fibrils are to be seen, with their free ends projecting into the cytoplasm (*fig. 23*).

As shown by the series of figures, the process of spindle development in the first division of Hesperaloe is essentially the same as that described for Gladiolus, Iris, and Disporum. On account of the scarcity of the material, the development of the spindle for the second divisions was not observed.

THE POLLEN MOTHER-CELLS OF HEDERA HELIX.

From the above description, it seems quite evident that there is a very striking resemblance in the method of spindle forma-

tion in Gladiolus, Iris, Disporum, and Hesperaloe. As these types are representative of related families, it is not surprising to find such a resemblance. This method of spindle development, however, is not peculiar to these families, as the following descriptions of the conditions existing in Hedera will show.

The young anthers containing the pollen mother-cells of *Hedera helix* are extremely small and difficult to handle. But after being fixed in the field and imbedded, the difficulties are mostly overcome, for the mother-cells stain very easily with the triple stain, and the various stages in the development of the spindle of the first and second division are readily obtained.

The mother-cells in Hedera are much smaller than the liliaceous plants, but the nuclei are relatively much larger. As division approaches, the amount of nuclear sap is very great, and as a result the nucleus occupies one-half the space of the cell. Before any kinoplasmic differentiation takes place, the cytoplasm presents a uniform granular reticulum, but this appears to be slightly denser in the vicinity of the nuclear membrane, suggesting the condition that exists in Cobaea and Gladiolus. As soon as the chromatin has segmented to form the chromosomes, the cytoplasm in contact with the nuclear membrane becomes differentiated into a thin weft of fibrils, which stain an intense blue. The development of the weft is essentially the same as that described for Gladiolus, Iris, Disporum, and Hesperaloe. It consists at first of only a few threads, which interlace with each other and run more or less parallel to the nuclear membrane. The fibrils nearer the membrane stain a very deep blue, but those farther out stain less, and as they merge into the surrounding orange-staining cytoplasm, they are slightly granular and are no longer to be distinguished from the reticulum of the latter (*fig. 24*). The origin of the fibrils of the weft is apparently due to the change in the structure of the threads of cytoplasm, as described in Iris, Disporum, and Hesperaloe. As in these plants, the weft is uniformly thick in the early stages of its formation, but it soon develops projections at irregular intervals, producing the primary cones of the multipolar figure (*figs. 25, 26*). As the primary cones grow outward, the fibrils composing

them no longer run parallel to the nuclear membrane or interlace with one another. They become long independent fibrils, projecting more at right angles to the nuclear membrane and converging at the apices of the cones. *Figs. 26* and *27* show several of these cones, nearly fully developed.

As the cones approach the completion of their development, the nuclear membrane suddenly disappears, and the fibrils at the base of the cones come in contact with the chromosomes. The fusion of the cones proceeds until there are two groups (*fig. 28*). The chromosomes are very numerous, and the mature spindle is consequently very wide at the equator. The usual connective and continuous fibrils are to be distinguished, but the mantle fibrils do not appear until the chromosomes begin their migration to the poles.

It is quite clear from the series of stages shown in *figs. 24* to *29* that the formation of the first spindle in Hedera is similar to that which occurs in Gladiolus, Iris, Disporum, and Hesperaloe in every essential particular.

In his work on Agave, Osterhout describes two distinct types of spindle formation in the two divisions preceding the development of the pollen. In the second division the spindle originates in a way that is absolutely different from that in the first. There is no weft surrounding the nucleus in the early stages, but instead there is a series of fibrils which radiate out from the nucleus, with their free ends projecting into the cytoplasm. Such a stage as this does not occur in the first division, and it is remarkable that two conditions so essentially different could be found in two succeeding generations of cells. With the idea of ascertaining whether any such difference as this existed in the two succeeding divisions of the mother-cell in Hedera, a very careful examination was made of every stage in formation of the second spindle. This proved quite conclusively that the spindles of the first and second divisions are formed in identically the same fashion.

Very little time elapses between the first and second divisions. As soon as the first spindle reaches the bipolar stage, the chromosomes move to the respective poles and unite, forming

two masses of chromatin at opposite sides of the cell. While this is taking place (*fig. 30*) numerous long mantle fibrils extend from the sides of the masses of chromatin and at the same time the continuous fibrils increase in number. The mantle fibrils, however, are not confined to the lateral position on the chromatin mass, but radiate from all sides of it. These radiating fibrils persist for a considerable time, even after the chromatin has secreted a nuclear sap and surrounded itself with a membrane. *Fig. 31* shows two mature daughter nuclei, with the chromatin in the spirem stage, each surrounded by a distinct membrane. The continuous fibrils between the two nuclei begin to disappear in the equatorial region of the cell, and each nucleus is completely surrounded by a system of radiating fibrils with their free ends projecting into the surrounding cytoplasm. When first observed, the writer mistook this condition for the radiating stage that Osterhout has figured in the formation of the second spindle in Agave. The two conditions are strikingly alike, but a careful study of the stages immediately preceding and following this showed conclusively that the radiating fibrils were the remnants of the first spindle and not the beginning of the second. As shown in the next stage (*fig. 32*), these radiating fibrils and the continuous fibrils disappear completely, and take no part whatever in the formation of the second spindle. As *fig. 32* illustrates, the resting period of the daughter nuclei is a very short one. The chromatin breaks up into chromosomes before the last of the continuous fibrils have vanished.

The first evidence of the beginning of the new spindle is the transformation of the cytoplasmic reticulum close to the daughter nuclei into a weft of fibrils completely surrounding each nucleus (*fig. 33*). In every detail the series of events that leads to the formation of the second spindles is identical with that of the first. Almost every stage in the sequence was carefully examined, and the second was found to be a duplicate of the first series. It will therefore be only necessary to mention the critical stages.

At first the kinoplasmic zone increases uniformly in thickness, and its fibrils run more or less parallel to the nuclear wall.

Very careful search was made for the radial condition described by Osterhout for the second spindle in Agave, but nothing like this was found. The fibrils are never radial at this stage.

Having reached a certain thickness the weft no longer increases uniformly, but grows out at irregular intervals from the primary cones of the spindle in identically the same fashion as it does in the formation of the first spindle (*fig. 24*).

SUMMARY.

1. In Iris the formation of the spindle is initiated by the transformation of the cytoplasmic reticulum close to the nuclear membrane into a weft of kinoplasmic fibrils, which forms a complete zone about the nucleus.

After increasing to a certain thickness, the zone projects outwards at irregular intervals, forming a series of cones which terminate in sharp points.

The cones apparently develop at the expense of the cytoplasmic reticulum into which they project, and as they grow the fibrils composing them lengthen and converge at the apex.

During the complete formation of the primary cones the nuclear wall persists.

Upon the breaking down of the nuclear membrane the cones fuse until there are two groups of them pointing in opposite directions.

The points at which the cones forming these groups meet at their apices become the poles of the bipolar spindle.

2. In Disporum the first indication of the spindle is the formation of a weft of kinoplasmic fibrils which partially surrounds the nucleus. As in Iris, the fibrils composing the weft are formed by the transformation of the cytoplasmic reticulum. Unlike Iris, the meshes of the weft do not run parallel to the nuclear membrane.

The weft increases irregularly, forming several projections which become the primary cones of the spindle. As they grow outward the cones become sharp-pointed and their fibrils are sharply defined. It is very clear that the kinoplasmic weft is of cytoplasmic origin.

After the cones have developed the nuclear wall breaks down, and the cones unite in two groups to form the bipolar spindle.

3. As in Iris and Disporum, the spindle in Hesperaloe originates from a weft of kinoplasm. The latter completely surrounds the nucleus and is of cytoplasmic origin. As in Iris, the fibrils of the weft run parallel to the nuclear membrane.

By growing out at irregular intervals the weft develops a series of sharp-pointed projections which become the primary cones of the spindle.

As the nuclear wall disappears, the cones collect in two groups and fusion at their apices brings about the bipolar condition.

4. In Hedera, as division approaches, the cytoplasm close to the nucleus becomes changed into a weft of kinoplasmic fibrils, which orms a zone completely surrounding the nuclear membrane.

This change in the form of the cytoplasm proceeds at intervals in such a way that the kinoplasmic zone appears to grow out in the form of projections. These projections terminate in sharp points and become the primary cones of the spindle.

As the cones grow outward the fibrils composing them become more sharply defined, elongate, and converge at their apices.

The events that follow are essentially the same as those in Iris, Disporum, and Hesperaloe.

The method of spindle formation of the second division is a duplicate of the first.

5. While the various methods of spindle formation described for the higher plants differ in certain respects, the resemblances between others are sufficiently great in warranting a classification of them. The following classification of the types is therefore suggested:

Type 1, represented by Gladiolus, Iris, Disporum, Hesperaloe, Hedera, Osmunda.

Type 2, represented by Cobaea, Passiflora, Lavatera.

Type 3, represented by Equisetum.

Type 4, represented by Agave.

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LITERATURE CITED.

1894. BELAJEFF, W. Zur Kenntniss der Karyokinese bei den Pflanzen. Flora **79**: 430.

1900. BYXBEE, E. S. The development of the karyokinetic spindle in Lavatera. Proc. Cal. Acad. Sci. III. Bot. **2**: 63.

1899. DAVIS, B. M. The spore mother-cell of Anthoceros. BOT. GAZ. **28**: 89.

1901. ——— Nuclear Studies in Pellia. Ann. Botany **15**: 147.

1897. DEBSKI, B. Beobachtungen über Kerntheilung bei *Chara fragilis*. Jahrb. Wiss. Bot. **30**: 227.

1893. FARMER, J. B. On nuclear division in the pollen mother-cells of *Lilium Martagon*. Ann. Botany **7**: 392.

1895. ——— Ueber Kerntheilung in Lilium-Antheren besonders in Bezug auf die Centrosomenfrage. Flora **80**: 56.

1898. GUIGNARD, L. Centrosomes in plants. BOT. GAZ. **25**: 158.

1898. ——— Les centres cinétiques chez les végétaux. Ann. des. Sci. Nat. Bot. VIII. **5**: 178.

1897. JUEL, H. O. Die Kerntheilungen in den Pollenmutterzellen von *Hemerocallis fulva*, und die bei denselben auftretenden Unregelmässigkeiten. Jahrb. Wiss. Bot. **30**: 205.

1898. LAWSON, A. A. Some observations on the development of the karyokinetic spindle in the pollen mother-cells of *Cobaea scandens*. Proc. Cal. Acad. Sci. III. Bot. **1**: 169.

1900. ——— Origin of the cones of the multipolar spindle in Gladiolus. BOT. GAZ. **30**: 145.

1897*a*. MOTTIER, D. M. Ueber das Verhalten der Kerne bei der Entwickelung des Embryosacks und die Vorgänge bei der Befruchtung. Jahrb. Wiss. Bot. **31**: 125.

1897*b*. ——— Beiträge zur Kenntniss der Kerntheilung in den Pollenmutterzellen einiger Dicotylen und Monocotylen. Jahrb. Wiss. Bot. **30**: 169.

1899*a*. NĚMEC, B. Ueber Kern- und Zelltheilung bei *Solanum tuberosum*. Flora **86**: 214.

1899*b*. ——— Ueber die karyokinetische Kerntheilung in der Wurzelspitze von *Allium Cepa*. Jahrb. Wiss. Bot. **33**: 313.

1898. ——— Ueber die Ausbildung der achromatischen Kerntheilungsfigur in vegetativen und Fortpflanzungs-Gewebe der höheren Pflanzen. Bot. Centralbl. **74**: 1–4.

1897. OSTERHOUT, W. J. V. Ueber Entstehung der karyokinetischen Spindel bei Equisetum. Jahrb. Wiss. Bot. **30**: 159.

1902. ——— Cell Studies 1. Spindle formation in Agave. Proc. Cal. Acad. III. Bot. **2**: 255.

1900. SMITH, R. W. The achromatic spindle in the spore mother-cells of *Osmunda regalis*. BOT. GAZ. 30: 361.

1896. STRASBURGER, E. Karyokinetische Probleme. Jahrb. Wiss. Bot. 33: 151.

1897. ——— Ueber Cytoplasmastructuren, Kern- und Zelltheilung. Jahrb. Wiss. Bot. 30: 375.

1900. ——— Ueber Reduktionstheilung, Spindelbildung, Centrosomen, und Cilienbildung im Pflanzenreich. Jena, 1900.

1897. WEBBER, H. J. Peculiar structures occurring in the pollen tube of Zamia. BOT. GAZ. 23: 453.

1899. WEIGAND, K. M. The development of the microsporangium and microspores in Convallaria and Potamogeton. BOT. GAZ. 28: 328.

1899. WILLIAMS, C. L. The origin of the karyokinetic spindle in *Passiflora coerulea*. Proc. Cal. Acad. Sci. III. Bot. 1: 189.

EXPLANATION OF PLATES XV AND XVI.

The figures were drawn with the Abbé camera, Zeiss apochromatic immersion obj. 12^{mm}, 1.30 ap., compensating ocular no. 6.

PLATE XV.— FIGS. 1–11. *Iris florentina.*

FIG. 1. A pollen mother-cell; cytoplasm in contact with nuclear membrane transformed into a weft of kinoplasmic fibrils, forming a narrow zone surrounding nucleus.

FIG. 2. Slightly older stage; kinoplasmic weft of considerable but not uniform thickness, preparatory to forming primary cones of spindle.

FIG. 3. Older; outward projections of the weft developed into a distinct sharp-pointed cone. Fibrils composing the cone no longer parallel to the nuclear wall, but directed outward and convergent at apex of cone.

FIG. 4. Like *fig. 3*, but also shows that cones do not develop simultaneously.

FIG. 5. Two cones nearly fully developed; a third beginning.

FIG. 6. Three primary cones of about the same size. Up to this stage nuclear wall is intact, taking no part in formation of kinoplasmic weft; nucleolus also persistent and now vacuolate.

FIG. 7. Nuclear wall and nucleolus have partly disappeared; fibrils at base of cones have grown inward and some have joined chromosomes.

FIG. 8. A characteristic multipolar figure; the three cones have evidently resulted from the union of several primary cones.

FIG. 9. Somewhat older stage showing further fusion of cones at their apices.

FIG. 10. Cones have united into two groups with their apices pointing in opposite directions, indicating the position of the bipolar spindle.

FIG. 11. Mature spindle.

PLATE XV. — FIGS. 12–17. *Disporum Hoekori.*

FIG. 12. Spore mother-cell showing transformation of cytoplasm into a weft of kinoplasmic fibrils not parallel to the nuclear wall.

FIG. 13. Later development of kinoplasmic zone; the weft not uniform but much more abundant on one side of nucleus.

FIG. 14. Weft in the form of irregular sharp-pointed primary cones; their fibrils very much elongated and convergent.

FIG. 15. Fibrils forming cones more independent of one another and more sharply defined.

FIG. 16. Nuclear membrane gone; cones united at apices; fibrils joined with chromosomes; the latter taking position at the equator.

FIG. 17. Mature bipolar spindle.

PLATE XVI. — FIGS. 18–23. *Hesperaloe Davyi*

FIG. 18. Pollen mother-cell, showing formation of kinoplasmic zone quite uniform in thickness.

FIG. 19. Later irregular outward growth of kinoplasmic zone; the meshes composing it point in the direction of the outward projection or primary cone.

FIG. 20. Nuclear wall breaking down; inward growth of fibrils from the base of the cones with which the chromosomes are now in contact.

FIG. 21. Typical multipolar spindle after entire disappearance of nuclear membrane.

FIG. 22. Cones collecting in two groups and uniting at their apices so as to indicate position of bipolar spindle.

FIG. 23. Mature bipolar spindle.

PLATE XVII. — FIGS. 24–34. *Hedera helix*

FIG. 24. Young pollen mother-cell showing early stage in the formation of kinoplasmic weft.

FIG. 25. Later stage of kinoplasmic zone, indicating by one-sided growth the beginning of one of the primary cones.

FIG. 26. Four more fully developed primary cones in the same plane; fibrils composing them much more clearly defined and convergent.

FIG. 27. Somewhat older stage with several cones in the same plane; fibrils very clearly defined and cones almost fully developed.

FIG. 28. Nuclear wall gone; chromosomes in contact with spindle fibrils; cones partially united in two groups indicating future position of bipolar spindle.

FIG. 29. Mature bipolar spindle. As there is a large number of chromosomes, the spindle is very wide at the equator.

FIG. 30. Chromosomes at the poles of spindle; nuclear wall not yet formed around daughter nuclei; many continuous fibrils between the daughter nuclei; also a series of short radiating mantle fibrils, which extend out in all directions from the masses of chromatin.

FIG. 31. Daughter nuclei with membranes; chromatin in spirem condition; continuous fibrils disappearing midway between the daughter nuclei; system of radiating fibrils persistent.

FIG. 32. All fibrils of first spindle have disappeared; chromosomes of daughter nuclei ready for second division.

FIG. 33. New weft of kinoplasmic fibrils forming a zone about each daughter nucleus, the first indication of spindles for second division.

FIG. 34. Weft growing out from one of the daughter nuclei to form primary cones of second spindle.

THE EMBRYO SAC OF CASUARINA STRICTA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. L.

THEODORE C. FRYE.

(WITH PLATE XVII)

IN the examination of the embryo sac of Asclepias (2) the writer was impressed with the long resting period of the egg between its fertilization and its first division. The difficulty of distinguishing a fertilized from an unfertilized egg suggested that in some cases in which fertilization was reported to take place after the division of the endosperm nucleus, an error had crept in, an unfertilized egg being mistaken for a fertilized one. If there is fertilization after endosperm division, the fate of the second male nucleus is an equally interesting question. This suggested a reinvestigation of the sac of Casuarina, the results of which are here presented.

The admirable paper of Treub (5) on Casuarina appeared in 1891. In a review of it by Chamberlain (1) in 1896, five years after it was published, the following suggestive statement is made:

> I have been deeply interested in Casuarina's embryo sac without antipodals, as I have been studying Salix and for more than a year was unable to discover any trace of antipodals. However, Salix has antipodals, as some of my preparations now prove. Some slides also show the fushion of polar nuclei to form the endosperm nucleus. There is no doubt that the antipodals of Salix are very transitory, but they are formed nevertheless. It may be that Casuarina has antipodals of this evanescent character. Since the technique betrayed by Treub's figures and text could be greatly improved, I should be glad to see the Casuarina sac studied again in much greater detail, in order that Treub's conclusion may receive additional confirmation or be corrected.

A résumé of the more essential features of Treub's paper is as follows: The species studied were *C. suberosa*, *C. Rumphiana*, and *C. glauca*. The pistillate flowers are naked, occurring in the axils of small bracts that form a cone-like cluster. Each pistil consists of two carpels whose inner surfaces soon fuse along

their lower part. Lateral placental outgrowths divide the ovarian cavity into two loculi, but from this central placenta two ovules usually arise, both of which, except in rare cases, form in the same loculus. The funiculi are curved downward so that the ovules lie with the chalaza in the base of the loculus and the micropyle toward the style. Several hypodermal cells ("primary mother-cells"), possibly archesporial in nature, become deeply situated on account of their own transverse divisions and form a multicellular sporogenous tissue, sharply differentiated laterally, as in pteridophytes. Later it is also well differentiated toward the micropyle, but not in the region of the chalaza, where a strong "intercalary growth" takes place, suggesting the origin of sporogenous tissue from cells not arising from the primary sporogenous cells. Of the sporogenous cells,[1] some function as spore mother-cells, some remain small and are soon resorbed, while in some species others become tracheids, recalling the formation of elaters among the liverworts. Those that function as spore mother-cells divide, each forming a row of four. Thus with pteridophytic sporogenous tissue, there is spermatophytic arrangement of megaspores. Some of these enlarge, forming embryo sacs, as many as a score of sacs being counted in a single ovule. They elongate more or less antipodally, some even penetrating the chalaza to the funiculus. Differing from almost all other spermatophytes, the functionless megaspores of Casuarina are not resorbed, but remain among the fully developed embryo sacs. Whatever the number of ovules in an ovary, only one is fertilized. The sacs in the unfertilized ovules enlarge, become binucleate, but form no antipodal prolongations. In the fertilized ovules not all the megaspores that enlarge form prolongations; those not centrally placed are often arrested early. In the fertile ovule only one sac is fertilized.

The formation of cells within the sac was not definitely traced,[2] but developing sacs with one nucleus, and sometimes with two nuclei, were found. A certain nucleus, of unstated

[1] Treub applies the term "sporogenous" cells to the tissue both before and after the formation of megaspores.

[2] It will be remembered that this work was done twelve years ago.

origin, near the micropylar end, is itself the egg, or develops the sex apparatus of one to four cells, usually three, one of which is the egg. The others (synergids), it is thought, are homologous with the neck cells of gymnosperms and pteridophytes. Treub draws this conclusion from their origin from a single micropylar cell with cellulose wall, and from their appearance. There are no antipodals.

This was the first case of chalazogamy reported. The passage through the chalaza is facilitated by the presence of the prolongations of the sterile megaspores, into which the tube enters, leaving them to reach the egg apparatus that is to be fertilized. It is stated, however, that the tube never enters the fertilized sac, but becomes attached to it at some point between the egg apparatus and the antipodal region. Sometimes a nucleus was observed in the tube, but never more than one.

The egg remained unchanged for some time before its fertilization. The exact moment of fertilization was not determined, but before it occurred the formation of a large number of endosperm nuclei had taken place, even as many as fifty. This conclusion was based on the fact that sacs were found which formed endosperm before the pollen tubes reached them.

Casuarina thus shows a megasporic sporogenous tissue reminding one of the pteridophytes, a number of embryo sacs suggesting gymnosperms, and "synergids" suggesting the canal cells of gymnosperms; and it was unique in the route of the pollen tube. These considerations led Treub to believe that the Casuarinaceae are intermediate between angiosperms and gymnosperms.

The species that I studied was *Casuarina stricta* Ait. The material was collected in California from introduced trees by Mr. Albert C. Herre and identified by him. It was killed in chrom-acetic acid; but unfortunately the pieces were large, and hence the killing was not rapid enough to catch cells in mitosis. Only the pistillate cones were secured. The ovaries were carefully teased out with needles and sectioned in paraffin. Longitudinal sections 5 μ thick and stained with safranin and gentian-violet were found to be the most satisfactory. The work was almost all done at night. Light was obtained from a gas-lamp

provided with a Welsbach mantle, and passed through an eight-inch globe filled with a half-saturated aqueous solution of copper sulfate. In this connection I wish to acknowledge my obligation to Mr. Alexander G. Ruthven and Miss Myrtilla M. Cook for assistance in the preparation of slides, etc.

The young cones, about 5 mm long, are covered with what appear to be hairs, but upon examination these prove to be the ends of the filiform carpels. The ovaries are flattened laterally, in contrast to the adaxial flattening of the wings in Pinus. The carpels show numerous crystals in a stratum of cells near their inner surfaces, a condition quite similar to that figured by Treub in *Casuarina suberosa*. The origin of the placenta was not traced, but the ovules arise laterally from a central placenta near its base, as Treub has reported in other species.

The two integuments arise normally (*figs. 1, 2, 18*) and leave a micropylar opening to the nucellus. About the time of their origin one would expect to find the archesporium. In the hypodermal layer at this stage there are certain cells (*fig. 3, a*) which may be interpreted as archesporial, but such an interpretation rests alone upon the form and size, and the relation of cells in that vicinity to each other later; the usual stains would not differentiate the cells either by darker stain or by showing larger nuclei. From *fig. 4* it seems that the archesporial cells divide by walls parallel to the surface. Possibly this is the division into primary wall and primary sporogenous cells, but there is only the evidence of other plants, which is insufficient. Mitosis in the succeeding divisions of cells *b*, *fig. 4*, showing presence or absence of reduction in chromosomes, would settle it, but no spindles were found. However, by further division of cells *a* or *b* or both, in *fig. 4*, a stage like *fig. 5* is reached. More transverse walls and greater elongation result in rows of cells being formed (*fig. 6*), of which the outer ones form the wall tissue and the inner ones the sporogenous tissue. The general arrangement of cells in rows, and the relative position of sporogenous tissue with regard to sterile tissue in comparison with the same in other spermatophytes, especially in the anthers, and in Selaginella, lead me to surmise that cells *a* and *b* of *fig. 4* give

rise, respectively, to wall tissue and sporogenous tissue. The occurrence of massive sporogenous tissue, as reported by Treub, is an indubitable fact. Its limits are well defined laterally by the larger cells and larger nuclei of the sporogenous tissue. At the ends it grades more or less into the surrounding parenchyma, and the cells near the micropile appear younger than those toward the chalaza. I am inclined to believe that the nucellus as it elongates carries with it the primary sporogenous cells, each of which leaves behind by its own division a train of sporogenous cells. The formation of sporogenous tissue near the chalaza from other than sporogenous cells, as suggested by Treub, was not observed, and is believed not to occur in *C. stricta*. According to Treub, some of the sporogenous cells absorb others, but nothing of the kind was found in *C. stricta*. Either this species differs from those studied by him, or the absorption of sporogenous cells has been confounded with the absorption of megaspores. *C. stricta* forms no tracheids in the sporogenous tissue, agreeing in this with Treub's report for *C. suberosa*. The cells of the sporogenous tissue are several times as long as wide (*fig. 6*), while later, when the embryo sacs begin to form, only approximately isodiametric cells are apparent. This makes me believe that Treub was right in his statement that the formation of four megaspores occurs here. A further reason for my conclusion, and a stronger one, is that later groups of four in a row are recognizable (*figs. 8, 9, 10*).

The differentiation of megaspores begins quite soon after their formation. Usually one of each group of four starts, but sometimes more (*figs. 10, 14*). Many get no further than an enlarged nucleus, while others reach various stages of development, up to an apparently fertilizable sac. A row of four, as in *fig. 10*, certainly presents a strong argument, if any further argument is required, for the megasporic nature of the cells composing such a row in angiosperms. The sterile megaspores are not all resorbed; but some certainly are, and it seems to me that most of them are. The number of sacs reaching maturity varies greatly in different ovules, but ranges from two to twelve. These are mostly those of central location, forming an axial core in the megasporic tissue.

The embryo sac passes through the normal 1, 2, 4, and 8-celled stages (*figs. 9, 10, 14, 15*). These stages were not all seen in sacs which eventually become fertilized, for among so many sacs which reach maturity one cannot tell which will be the favored one until it is approached by the pollen tube. However, if one finds all these stages in embryo sacs arrested in various degrees of development, one may with reason conclude that the one later fertilized passed through the same stages, especially since some which remain sterile reach a development equal to that of the one later fertilized, so far as could be determined. As many as twelve, each having a fully developed egg apparatus, were found in a single ovule.

Within well-developed sacs three cells are organized at the micropylar end, forming the egg apparatus (*figs. 14, 16, 17*). In *fig. 14, C*, the cells have not yet collected definitely enough to make it certain which will form the egg apparatus. It is surmised, however, that three of the cells *a*—*d* will function as such; *e* is probably the antipodal polar. From *figs. 10, 14, 15, 16*, I can see no escape from the conclusion that the egg apparatus is normal in its origin. These figures are not exceptions chosen here and there to prove a point. They can easily be duplicated. *Fig. 16* is indeed the type of a fully developed sac in this species. An examination of the egg apparatus in *figs. 15, 16, 17* shows that there is considerable variation in the form of the cells composing it in the different sacs. The egg itself cannot be distinguished from the synergids in most cases. Sometimes cases occur showing less than three cells in the egg apparatus, but these are few in number, and it seems to me do not warrant a conclusion that Casuarina is different in this respect from other angiosperms.

Normally there are three antipodals. Comparing *figs. 10* and *14*, the latter is evidently the older group of megaspores. What is seen in *fig. 14, C*, is just what would be expected in the development of a normal sac. Of the eight cells in *fig. 14, C*, three (*f*) are collected in a depression in the antipodal region, just as one might expect, and about them is massed a quantity of protoplasm almost, if not completely, separated from the rest

of the protoplasm of the sac, strongly suggesting the separation of these cells by a wall. Comparing now *fig. 14, C*, with *fig. 15*, a slightly older sac, the antipodals in the latter certainly cannot be questioned. The whole sac is typical enough of angiosperms to serve as a conventional prefertilization sac. However, as has been remarked, *fig. 16* is more typical of the sac of *C. stricta*. In the older sacs (*figs. 16, 17, 20*) these antipodals resemble the unabsorbed megaspores very much, and could easily be mistaken for them. This might account for their reported absence, unless other species differ in this respect from *C. stricta*.

Sometimes, however, no antipodals were found (*fig. 21*), and the reason for this may be considered. Some of the sacs develop long antipodal prolongations (*figs. 14, 17, 20*), and these do not always appear at the same time. *Fig. 11, a* shows one already under way when the sac is in the 2-celled stage, and 4-celled stages were also found showing the beginning of antipodal prolongations. *Fig. 13* may be developing one at *a*, although that cannot be said with certainty. In a case like *fig. 11*, when the sac reaches the 8-celled stage and the antipodals settle at some point, where will they likely be found? If they seek the antipodal end, they will likely slip into the antipodal prolongation and perhaps be found somewhere within that. At least such a thing seems quite possible. The antipodal prolongations, however, are long tortuous tubes, very much entangled with their fellows. It is almost impossible to trace a definite one to its end with certainty. Much more is it difficult to determine the number of nuclei within, when above and below it are scattered unresorbed undeveloped megaspores. There are nuclei within these prolongations in some cases in which antipodals are wanting, but I was not certain of the number in any case. However, in one case there were three cells (*fig. 14, D, h, i, j*) at various distances down the tube. If in this sac the polars had already united, all the nuclei are accounted for. Sometimes, however, the antipodal prolongations are not formed until late in the history of the sac (*figs. 14 C, 15*). If it occurs after the antipodals have become inclosed by walls and perhaps adhere to the walls of the sac (*fig. 16, a*), their presence in the body of the sac,

notwithstanding the presence of an antipodal prolongation, is explained. Thus I believe we have the solution of the antipodal problem in Casuarina. Some of the antipodal prolongations grow so long that they penetrate the chalaza, occasionally passing slightly beyond it into the funiculus.

The location of the polar nuclei is quite various. Like the antipodals, they seem occasionally to pass into the antipodal prolongations (*figs. 14 D, 17*), and are lost in the maze of tubes. Sometimes only one was found (*fig. 16, c*), but in this case the polars may have fused and this is the endosperm nucleus. The sac then, except for the antipodal prolongation and its consequent effect upon the location of the antipodals and the endosperm nucleus, seems to be normal in its development.

Only one pollen tube penetrates a flower, hence only one ovule is entered and only one embryo sac in that ovule is fertilized. The favored sac was in all the observed cases near the micropylar end of the megaspore group. The pollen tube enters the ovule as Treub has stated (**5**). Coming down the central placenta (*fig. 18*), it wanders somewhat in the region where the funiculus has its origin, as though the attractive influence, or whatever it is that guides it, were not sufficiently strong to guide it with certainty. The tubes again frequently branch just before entering the chalaza (*fig. 18, b*). Sometimes the branches reach the surface, as Treub says, and he suggests two possible reasons for the branching: (*a*) for aeration; this is suggested by their often reaching the surface; (*b*) for holdfasts to anchor the tube firmly before it makes its entry into the nucellus. Neither of these appeals to me very strongly, and for the latter I see no reason at all. The cause is probably the same as that which causes wandering at the point of entry into the funiculus.

The tube seems to enter the prolongation of one of the embryo sacs and thus finds an easy passage through the chalaza. The plugs of cellulose in the tubes at intervals, as reported by Treub, are quite rare in *C. stricta*, and when present are short, resembling more a thick transverse wall than a plug. In the maze of tubular antipodal prolongations I was not able to follow the pollen tubes with certainty, and cannot therefore say whether

the end is separated from the main body, as Treub claims, or not. When it approaches the sac that it ultimately fertilizes, it is sometimes free (*fig. 20*), and sometimes apparently within the prolongation of the very sac whose egg apparatus it is destined to reach (*fig. 21*). I doubt whether there is any fixed path within the nucellus for the tube. It probably follows the path of least resistance so long as it leads in the direction whence comes the guiding stimulus, whatever that may be.

The sperms were observed near the chalaza in several preparations, as small rounded nuclei accompanied by the tube nucleus (*figs. 18, 19*). They were again seen, still spherical, in the tube near the sac about to be fertilized (*fig. 21*), and here too the tube nucleus was close behind them. This nucleus is easily distinguished from the sperms by its comparatively large size. In *fig. 20* the sac, which is evidently quite near the point of fertilization, shows only two antipodals, and there is one nucleus missing in the egg apparatus. The nuclei *p* are probably the two polars. It would be possible to regard these as two endosperm nuclei, but no reason for doing so appears.

Fig. 21 is a case of "double fertilization." In this the tube, or its contents, apparently entered by way of the antipodal prolongation. The sperms are crescentic bodies, one slightly larger than the other. The two polar nuclei have not yet united. I see no reason for any other interpretation of the two polars; if they are endosperm nuclei, we have a unique case in the fusion of a sperm with endosperm. Which of the three micropylar nuclei is the egg I cannot say, but it is probably the one containing the larger spherical nucleus, or that containing the elongated nucleus. No antipodals are in evidence, but they are probably in the antipodal prolongation. The sperms evidently elongate within the sac or very near it, as in Asclepias (**2**).

I am convinced that no such endosperm formation before fertilization occurs as Treub thought, and my reasons are as follows:

1. The cases of fertilization observed (*figs. 20, 21*) show no endosperm.

2. The pollen tube sometimes enters the ovule before the embryo sacs are ready for fertilization. In one case pollen

tubes were found in the funiculus before the division that results in the four megaspores, and at various times tubes had passed the chalaza while there was no sign of endosperm in the sacs. Usually when a tube gets close to the sac its penetration is rapid, and Treub says its growth within the nucellus is rapid. It seems, then, that there would not be time for a great development of endosperm between the time of the entry of the tube into the chalaza and its entry into the sac.

3. Inferring the exact time of fertilization from the presence of pollen tubes is not conclusive. Anyone who has tried to distinguish a pollen tube in the confused strand of tubular antipodal prolongations will readily understand the difficulty of determining without a doubt what is tube and what is sac. Even if tubes are seen, it is not an easy matter to tell whether they are young or old, and it must have been much more difficult with teased preparations.

4. Very little was said or known twelve years ago about the retarded division of the egg. Now it is known that the angiosperm egg often rests for a time after its fertilization, while the formation of endosperm begins at once. It was the writer's good fortune to study such a phenomenon in the embryo sac of Asclepias (**2**), in which the exact time of fertilization was observed, and the egg rested after fertilization until the endosperm had passed its 16-celled stage. If the exact time of fertilization had not been seen, one would have been apt to judge the resting fertilized egg to be an unfertilized one, and would have been inclined to say that endosperm division took place before fertilization. Johnson's study of the Piperaceae (**3**) has brought to light the same resting period in the egg of *Piper medium*. He figures a sac with twenty-two endosperm nuclei in cross-section, already walled off, and the egg still undivided. In the same paper he says of *Heckeria umbellata* that the embryo sac becomes filled with cellular endosperm before the egg divides. It is only fair to add, however, that fertilization was not observed in these species, but the appearance of the egg leaves little doubt of its fertilization long before it divides.

5. The fact that Treub found a definite wall about the egg in

most cases suggests a post-fertilization stage. The rounded form of his figures of eggs also suggests the same.

Unfortunately, the material at hand showed no embryos nor endosperm, the oldest showing that the pollen tubes had reached the sac. It would have been quite interesting to note the condition of the egg during endosperm development. But if one supposes that Treub mistook a fertilized egg for an unfertilized one—a thing which might even be possible with the technique of today, to say nothing of twelve years ago—and if he further mistook a discharged pollen tube for an undischarged one, the formation of endosperm before fertilization would be eliminated from his own account. It will be recalled here that he himself could not be certain about seeing nuclei in the pollen tube except in a few cases, and in no case is more than one suggested. From the size of the tube nucleus (*fig. 20, t*) one is led to conclude that he saw it rather than a sperm.

A summary of my results with *C. stricta*, as compared with Treub's with *C. Rumphiana*, *C. glauca*, and *C. suberosa*, may be stated as follows:

There is agreement as to the bilocular ovary, the presence of two ovules in an ovary and both in the same loculus, the presence of two integuments and a micropyle, the upright ovules that arise laterally from the central placenta, the multicellular archesporium consisting of a hypodermal plate of cells, the massive sporogenous tissue, the division of each spore mother-cell to form four megaspores, the numerous mature sacs in an ovule, the long antipodal prolongations of the sacs, the fertilization of only one embryo sac in every ovary, and chalazogamy.

There is disagreement as to the origin of the sporogenous tissue, in *C. stricta* all of it arising from the hypodermal archesporial plate, while Treub believes that some sporogenous tissue near the chalaza does not arise from this plate; as to the resorption of sporogenous cells, which Treub claims, but I was not able to observe; as to the sequence in the formation of the embryo-sac structures, which differs in no way in *C. stricta* from the sequence usual among angiosperms; as to the character of the egg-apparatus, which differs in no way in *C. stricta* from that

of other angiosperms; as to the presence of antipodals, which are certainly present and normal in number in *C. stricta;* as to the relation of endosperm formation to the time of fertilization, Treub reporting much endosperm before fertilization, and in *C. stricta* fertilization clearly taking place before endosperm-formation.

The additional facts, not observed by Treub, are the occurrence of "double fertilization," and the presence of two sperms, spherical in the pollen tube and crescentic in the sac.

My thanks are due to Professor John M. Coulter and Dr. Charles J. Chamberlain for valuable assistance in the prosecution of the work and in the publication of the results.

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LITERATURE CITED.

1. CHAMBERLAIN, C. J., BOT. GAZ. **21**: 374. 1896.
2. FRYE, T. C., A morphological study of certain Asclepiadaceae. BOT. GAZ. **34**: 389–413. *pls. 13–15.* 1902.
3. JOHNSON, D. S., On the development of certain Piperaceae. BOT. GAZ. **34**: 321–340. *pls. 9–10.* 1902.
4. STRASBURGER, E., Lehrbuch der Botanik 409. Jena. 1900.
5. TREUB, M., Sur les Casuarinées et leur place dans le système naturel. Ann. Jard. Buitzenborg **10**: 145–231. *pls. 12–32.* 1891.

EXPLANATION OF PLATE XVII.

All drawings were made with a Bausch & Lomb camera lucida, $\frac{2}{3}$, $\frac{1}{6}$, $\frac{1}{12}$ (oil) objectives, and nos. 1 and 2 oculars. The figures have been reduced one half, but the original magnifications are given.

Casuarina stricta Ait.

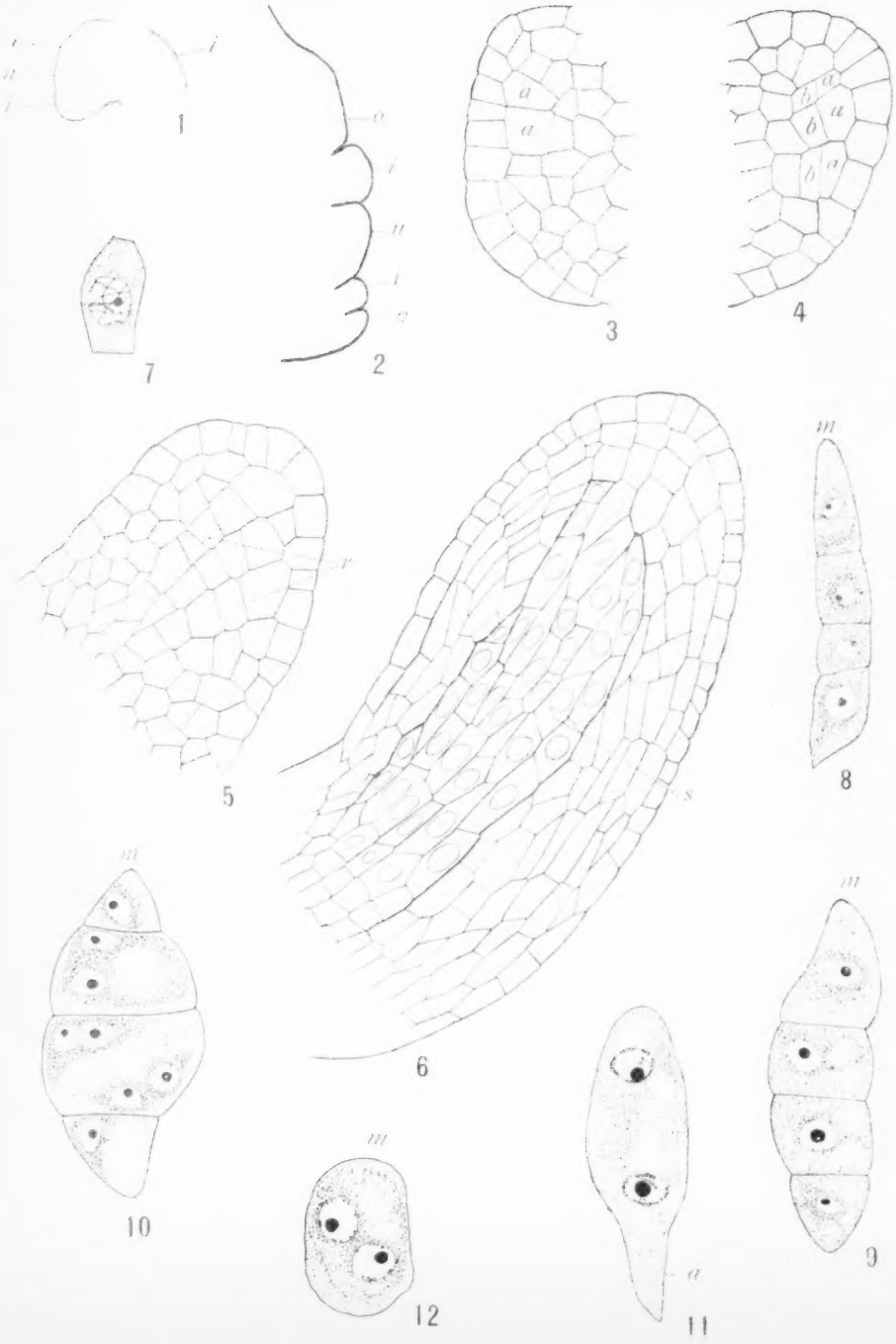
FIG. 1. Young ovule: *n*, nucellus; *i*, inner integument; *l*, loculus without ovule. × 207.

FIG. 2. Ovule: *n*, nucellus; *o*, outer integument; *i*, inner integument. × 140.

FIG. 3. Nucellus about same stage as in *fig. 2; a*, cells which may be archesporium. × 1366.

FIG. 4. Nucellus with hypodermal periclinal wall-formation, suggesting that *a* may be primary wall cells, and *b* primary sporogenous cells. × 1366.

FIG. 5. Nucellus, suggesting that interior cells *r* arise from hypodermal cells at apex. × 1366.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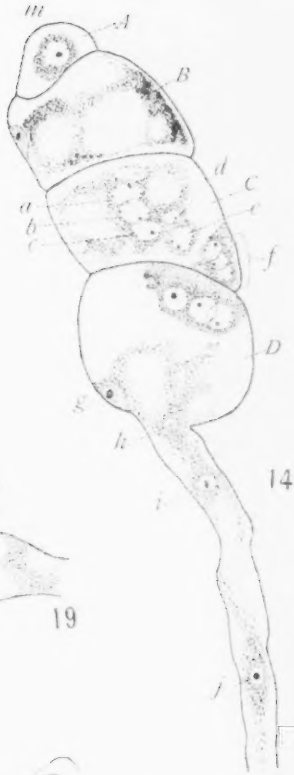

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FIG. 6. Nucellus: *s*, massive sporogenous tissue within, with well defined lateral limits. × 900.

FIG. 7. Spore mother-cell about to divide, showing chromatin threads; the cells are longer, the section is diagonal. × 1950.

FIG. 8. Row of four megaspores; *m*, micropylar end. × 1950.

FIG. 9. Row of four megaspores, the middle ones enlarging; *m*, micropylar end. × 1950.

FIG. 10. Row of four megaspores in various stages of embryo sac formation; *m*, micropylar end. × 1950.

FIG. 11. Two-celled embryo sac; antipodal prolongation (*a*) already begun. × 1950.

FIG. 12. Two-celled embryo sac; *m*, micropylar end; no well defined antipodal prolongation. × 1950.

FIG. 13. Four-celled embryo sac; *a*, possibly beginning of antipodal projection. × 1950.

FIG. 14. Row of four megaspores derived from one spore mother-cell and older than those in *fig. 10*; *m*, micropylar end; *A*, arrested megaspore; *B*, megaspore probably arrested after some internal cell division, but now disintegrating; *C*, 8-celled sac; *a*, *b*, *c*, *d*, will probably form egg apparatus and micropylar polar; *e*, probably antipodal polar; *f*, antipodals with suggestion of wall formation; *D*, 7 or 8-celled sac with antipodal prolongation: *h*, *i*, *j*, probably antipodal and polar or endosperm cells. × 1950.

FIG. 15. Eight-celled embryo sac; *a*, antipodal; *p*, point where antipodal projection may be expected to arise; *po*, polar nuclei. × 1950.

FIG. 16. Typical embryo sac without the long antipodal prolongation; *e*, endosperm nucleus; *a*, antipodals. × 1950.

FIG. 17. Embryo sac with more elongated cells in egg apparatus; only two antipodals found; *a*, polar nuclei or one endosperm and the other antipodal. × 1950.

FIG. 18. Pollen tube approaching the nucellus; *b*, branch of tube; dotted line bounds sporogenous tissue. × 140.

FIG. 19. Part of *fig. 18* enlarged; *t*, tube nucleus, *s*, sperms. × 1366.

FIG. 20. Pollen tube just having reached the embryo sac; *pt*, pollen tube; *t*, tube nucleus; *s*, sperms; *a*, antipodals; *p*, polars, one nucleus in egg apparatus and one antipodal missing. × 1950.

FIG. 21. A case of double fertilization; *s*, sperms; antipodals not found in this preparation. × 1950.

ON THE GAMETOPHYTES AND EMBRYO OF TAXODIUM.

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF THE JOHNS HOPKINS UNIVERSITY, No. 1.

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(WITH PLATES I–XI)

(*Concluded from p. 27*)

FORMATION OF VENTRAL CANAL NUCLEUS.

MURRILL ('00) has recently described in Tsuga a peculiar method of spindle-formation in the division of the central cell of the archegonium. He finds a kinoplasmic area in contact with the inner side of the nucleus just before its division. Fibers begin to grow from this area into the nucleus, pressing before them the nuclear wall. They gradually extend until they come to occupy the greater part of the nuclear cavity, and are then joined by similar fibers which have come in from the opposite pole to form the prophase of the spindle. These observations I cannot confirm in Taxodium. *Figs. 76–90* show this division in detail. As already stated, fibers pass around the nucleus from the kinoplasmic areas or aster and merge insensibly into the nuclear wall. The nuclear wall is frequently considerably drawn in at a point opposite the kinoplasmic body (*figs. 76, 78*), but no strong fibers can be seen extending from one to the other at this point. In fact, this collapse is generally more noticeable in the early stages of preparatory changes. Murrill ('01) finds such fibers, which he concludes have caused the depression of the nuclear wall.

The arrangement between aster and nucleus at this time may be best compared to that between the car of a balloon and the bag above it, the ensheathing fibers of the nucleus terminating in the aster representing the ropes around the balloon connecting it with the car below. *Fig. 76* shows the beginning of the changes in the nucleus which lead to the formation of the spindle.

Synapsis has occurred, and the nuclear reticulum forms a dense tangle near the nucleolus. The latter can now be distinctly seen to be of compound structure, and from it threads can be traced into the network. Fine threads also connect the conspicuous central tangle with the nuclear walls. Such a synapsis stage is described by Murrill in the nucleus of the central cell of Tsuga. In *fig. 72* the reticulum has begun to move back into its original position. The nucleolus is now distinctly fragmented into a number of granules of apparently equal size, which gradually become more and more separated into a broken ring or coiled thread (*figs. 78–80*). These granules retain the deep red stain characteristic of the nucleolus in previous stages. The ring, or thread, is now broken up more and more into separate parts and distributed near the periphery of the nucleus (*figs. 81–84*) and the reticulum of the nucleus begins to arrange itself for the formation of the spindle (*figs. 83–85*). The fibrous connections between the reticulum and the nucleolar thread are to be noticed at all stages of its distribution.

The red-staining granules derived from the nucleolus have not lost their identity at any stage. They become gradually elongated and thin (*figs. 85, 86*), and thus approach more and more the characteristic structure of the chromosomes. The fibers of the reticulum draw together at different points of the nucleus and certain centrally placed ones become distinguishable as spindle fibers, while the mantle threads pass gradually into the unmodified reticulum of the nucleus. The granular nature of the spindle is evident even at so late a stage as *fig. 86*. The nuclear wall has meanwhile disappeared, but its position is indicated by the arrangement of the fibers until the anaphase stage of division (*fig. 87*). The chromosomes, as they are drawn apart, are of the usual V or U shape (*fig. 87*). The transformation of the nucleolus into the chromosomes may be followed without interruption through its whole course, not only by reactions in staining, but in serial development.

Chromatin nucleoli have frequently been described, but principally among the lower plants. Strasburger ('00) in his recent work devotes considerable space to the discussion of the part

played by the nucleolus in the formation of the spindle. He reviews the present knowledge of the subject, and while acknowledging the chromatin character of the nucleolus in a few cases, expresses himself as strongly inclined toward the view that in the higher plants at least it is of kinoplasmic or spindle-building material. Nucleoli of chromatin character have been described in Corallina by Davis ('98), in Spirogyra by Mitzkewitsch ('85), in Bignonia by Duggar ('99), and in a number of other plants. That the nucleolus of the central cell in Taxodium is directly transformed into chromosomes seems to be evident from the figures given, and I think we may be equally sure of the intranuclear origin of the spindle. The kinoplasmic mass at the tip of the spindle seems to serve merely as a point of attachment for the spindle fibers, its numerous radiations making a firm foundation for the orientation of the spindle, as suggested by Murrill ('01).

The nucleus of the central cell, just before its division, is generally situated not far from the tip of the archegonium, but it is often found as much as a third of the way down. In such cases the central vacuole, which is now much smaller, lies nearer the base of the archegonium. The wall of the nucleus is at the very surface of the cell (*figs. 66, 78*), and it is often impossible to distinguish any protoplasm between nucleus and surface. In *figs. 88* and *89* there is to be noticed in the center of the spindle a broad zone which is composed of numerous granules. In Flemming's triple this zone stains a deeper violet than the other parts of the spindle, and occupies the position at which we might expect to find a cell plate. No cell plate is formed, however, and the whole spindle fades away into the cytoplasm of the cell. At the surface end of the spindle shown in *fig. 87* a small aster has appeared. The daughter nuclei are formed in the centers of these asters (*fig. 88*), and as they increase in size the kinoplasm is collected more and more on the sides toward the spindle (*figs. 89, 90*). In this way the egg and ventral canal nuclei are both furnished with a tuft of kinoplasm on their inner faces. Other tufts may be located at different positions around the egg nucleus (*fig. 90*), but in

later stages the egg nucleus is nearly always furnished with but a single tuft on the side toward the base of the archegonium. The spindle may be situated in every position in reference to the axis of the archegonium, parallel (*fig. 87*), perpendicular (*fig. 88*), or inclined (*figs. 86, 89*), but the inner pole is always located in the center of the aster. The spindle may extend either up or down from the inner pole, and the ventral canal nucleus may thus be placed either above or below the egg nucleus (*fig. 91*). The archegonium to the right in *fig. 92* shows a ventral canal nucleus situated nearer the base than the tip, and in the archegonium to the left the ventral canal nucleus occupies a nearly central position, the egg nucleus lying even lower. It is only rarely that the ventral canal nucleus is situated at the very tip of the egg. Such a position is shown in *figs. 87* and *90*.

This formation of the ventral canal nucleus in any region other than near the tip of the archegonium has not been described in any other gymnosperm so far as I am aware. This peculiarity in Taxodium seems to be an acquired character for the protection of the ventral canal nucleus during fertilization, for, as we are to see later, it is to play a part in the subsequent history of the egg. In most gymnosperms the ventral canal nucleus is furnished with a certain amount of protoplasm of its own which is distinctly separate from that of the egg. Arnoldi ('00) lays stress on what he calls the absence of a ventral canal cell in Cephalotaxus. He considers the ventral canal cell lacking because no wall is formed between the ventral canal nucleus and the egg. In this case, however, a certain amount of protoplasm becomes disorganized around the ventral canal nucleus, and swelling up is said to burst open the neck of the archegonium. If this is the case, the disorganizing protoplasm may be considered as belonging to the ventral canal nucleus, and a ventral canal cell could not strictly be said to be absent.

In Taxodium, however, not even a cell plate is formed, and the ventral canal nucleus lies perfectly free in the cytoplasm of the egg without a distinct protoplasmic area of its own. A ventral canal cell in the strict sense is therefore lacking here.

From Strasburger's ('79) account it seems probable that this is equally true in the Cupresseae. Ikeno ('01) has well remarked that the important point is the division of the nucleus and not the separation of a small amount of protoplasm from the egg. Arnold ('99) denies the occurrence of even a ventral canal nucleus in Sequoia.

The ventral canal nucleus remains closely applied to the surface of the egg and is somewhat flattened or compressed. It does not go through the peculiar changes which occur in the egg nucleus before fertilization, but having reached the condition shown in *fig. 90* does not develop much further until after the fertilization of the egg. It is furnished with a chromatin reticulum and an evident nucleolus. The ventral canal nucleus has usually been described as undergoing disorganization soon after its formation, sometimes reaching a resting condition, but generally never developing further than the first stages of this condition (Blackman, '98; Ikeno, '98; Murrill, '01, among others). Chamberlain ('98) figures a well-developed nucleus in the young fertilized archegonium of *Pinus Laricio*, which closely resembled the egg nucleus and which is, as he suggests, in all probability the ventral canal nucleus. Very recently Ikeno ('01) has described a large nucleus in the tip of the egg of Ginkgo and called it a ventral canal nucleus. He also calls attention to the possibility that a persistent ventral canal nucleus may have been mistaken for the extra male nucleus among previous observers. It has also probably been figured as the functional male nucleus.

The position of the ventral canal nucleus in Taxodium at some protected place on the side of the archegonium has preserved it from destruction during the entrance of the sperm cell, and as the fusing male and female nuclei approach the base of the archegonium the ventral canal nucleus begins to extend into the center, and by amitotic division it usually gives rise to the several nuclei of different sizes which occupy the upper half of the egg (*figs. 107, 112*). If the egg is not fertilized, the ventral canal nucleus generally remains unchanged in its original position (*fig. 107*), but it not infrequently increases in size and moves

nearer the center of the egg at about the time that those of the fertilized archegonia are dividing amitotically. In these cases it does not divide, but increasing greatly in size comes to resemble the egg nucleus just as in the case described by Chamberlain ('98) (*fig. 114*). Indications of amitotic division may be sometimes seen in the ventral canal nucleus in unfertilized archegonia (*fig. 113*), but such cases are rare. The development of the ventral canal nucleus in fertilized archegonia is not the exception, but the rule. In almost all cases in which there is a proembryo present there are to be found in the upper part of the archegonium a varying number of nuclei of different sizes which have been derived from the ventral canal nucleus (*figs. 115, 116*). In some cases, as would naturally follow when the ventral canal cell is cut off far down the archegonium, the nuclei derived from it may occupy a position near the base, and consequently near the proembryo. *Fig. 118* is such a case. Here, the ventral canal nuclei are sharply distinguished from the nuclei of the embryo (only one of which is shown) by the entire absence of the starch sheath characteristic of the latter. The ventral canal nuclei are usually separated from the proembryo by a distinct area of disorganizing protoplasm, but they themselves seem to retain a part of the protoplasm at the tip of the archegonium which is not disorganized until much later (*fig. 116*).

DEVELOPMENT OF THE FEMALE NUCLEUS.

The female nucleus in its very young stages is shown in *figs. 88* and *89*. It develops more rapidly than the ventral canal nucleus and goes through the peculiar changes of structure which have already been described in more or less detail by others. The chromosomes spin themselves out into a reticulum which is apparently often arranged in a spiral form (*fig. 89*). A nucleolus begins to appear early. At the stage of *fig. 89* the nucleus is not yet furnished with a distinct membrane, but in *fig. 90* the wall has appeared. There is first seen at this stage a finely granular substance which has been called metaplasmic substance by Strasburger and some recent workers. From the subsequent behavior of this substance, it would be better described

as kinoplasm than as metaplasm, but as the former word is overworked I shall follow Chamberlain ('99) and speak of it as linin, from which it does not seem to differ. It is at first entirely distinct from the reticulum, and is only very slightly stained in Flemming's triple. The nucleolus increases in size and the linin granules become more abundant as the nucleus develops. The reticulum still remains perfectly distinct from the granular substance and stains a bright red in safranin. The nucleolus is of quite a different character from the nucleolus of the central cell previously described. It becomes larger and larger until, at the time of fertilization, it is very conspicuous (*fig.* 100). When deeply stained, it seems to be entirely homogeneous, but on washing out a fine alveolar structure is to be seen. This does not in the least recall the irregular compound nucleolus of the central cell, and from the entirely different behavior of these two nucleoli during cell division it is evident they are of a different nature. The large nucleolus of the egg nucleus may be called the plastin nucleolus, while that of the central cell is a chromatin nucleolus. The plastin nucleolus of the egg nucleus seems to loose its stain more easily at one time than at another, as it is frequently found almost colorless. This loss of staining quality may be due to fluctuations in the amount of plastin material inclosed in its honey-comb-like structure during the active stages of development. This seems more probable, as it is often found when unstained in a collapsed condition, a distinct but thin shell being always present.

At the time of fertilization the female nucleus may vary considerably in its structure. Sometimes the linin material remains finely granular up to the time of fertilization. In such cases it is easily distinguishable from the chromatin reticulum, which on account of the huge size of the nucleus is now relatively scarce. The large plastin nucleolus is always present and is not connected in any way with the reticulum. This is another character which distinguishes it from the chromatin nucleoli already described. It is more frequently the case that the linin substance of the nucleolus, before the entrance of the male nucleus, has become grouped into an abundant reticulum, upon which granules of

various sizes are deposited (*fig. 101*). The larger of these linin granules take the red stain, and thus become indistinguishable from the chromatin masses of the nucleus. At no stage in the development of the egg nucleus is it without a distinct reticulum. Whether the chromatin reticulum contracts to form separate chromatin masses or whether it remains as the coarser part of the reticulum shown in *figs. 100* and *101* seems uncertain.

Chamberlain ('99) and Blackman ('98) have minutely described the development of the female nucleus in *Pinus Laricio* and *Pinus sylvestris*, respectively. The former describes the complete disappearance of the nuclear reticulum at two stages of the development of the nucleus. At the time of fertilization the chromatin is all grouped in the center of the egg nucleus, the remainder being occupied by the finely granular linin substance. This condition would not be so different from the case in Taxodium if the chromatin reticulum of the latter should resolve itself into chromatin nucleoli before the organization of the linin substance into a distinct reticulum. Such a condition, however, has not been found. In the mature egg nucleus the number of small nucleoli which take the red stain with safranin is sometimes no larger than could be supplied by the chromatin of the nucleus, but when the linin substance becomes collected into large granules, which is not at all unusual, they also take the red stain and cannot easily be distinguished from the chromatin nucleoli. Their color, however, is usually a more purplish red than is the case with the chromatin nucleoli, and if the washing is continued they are the first to lose the reddish stain.

FERTILIZATION.

We left the pollen tube after describing the formation of the male cells. The divisions of the central cell of the archegonium and of the central cell of the pollen tube occur simultaneously, or almost so, in every case observed, and in this respect again resemble the Cupresseae (Strasburger, '79). Fertilization occurs in a very short time after the completion of these divisions. As stated in my previous note, both sperm cells may enter one archegonium, but this is by no means always the case, in fact

not generally so; and when it does occur it may be considered as a failure to secure the results aimed at. When several pollen tubes have reached the archegonial group (as many as five have been noticed) the entrance of two or more sperm cells into an archegonium is not unusual, but when the number of tubes is only one or two it less often occurs. Pollen tubes sometimes are so abundant that all cannot pass into the depression above the archegonial group. Some then remain in different positions around the tip of the prothallium, and are often to be seen unchanged after their more fortunate neighbors have fertilized the archegonia. The central cell of such pollen tubes often divides at the same time with those over the archegonia, but in some cases where they are small and badly nourished the central cell does not divide at all.

In addition to the one or two sperm nuclei that enter the archegonium the disorganized remains of the stalk and tube nucleus with their surrounding protoplasm are also swept in, along with what is left of the neck cells. Prothallial nuclei are also sometimes thrown in, and quite a collection of such heterogeneous material may often be seen in the archegonial tip above the protoplasm of the egg. Most observers who have described the discharge of extra sperm nuclei or vegetative cells into the fertilized archegonium have made no distinction between entrance into archegonium and entrance into egg. Webber ('97) says that several spermatozoids may enter a single archegonium in Zamia, but that only the one that is used in fertilization actually enters the cytoplasm of the egg, the others remaining above and free in the cavity of the archegonial tip. Ikeno ('01) calls attention to this point, and finds that in Ginkgo the supernumerary spermatozoids do not enter the cytoplasm of the egg, but remain distinct from it, even if actually pressed into its surface. He also mentions the possibility that certain nuclei in the tip of the archegonia, that have in previous cases been described as derived from the sperm cell, are probably the results of amitotic division of a persistent ventral canal cell. These observations of Webber and of Ikeno I can positively confirm in Taxodium. The supernu nerary sperm cells remain separate from the cytoplasm of the

egg, and may be long distinguished as they slowly disorganize (*figs. 104, 110*).

The functional sperm cell in its course to the egg nucleus is shown in *figs. 100* and *101*. Its protoplasm becomes intimately connected with that of the egg, but its identity is not lost at any stage. The starch sheath still remains in close contact with the sperm nucleus, and as its boundary touches the wall of the female nucleus it spreads around it more and more, while the sperm nucleus in its center finally comes in contact with the nucleus of the egg (*fig. 102*). This starch sheath of the sperm nucleus furnishes the sheath which is characteristic of the fusion nucleus.

Strasburger has several times spoken of the sudden appearance of starch in the fertilized egg of the Cupresseae. In his *Neue Untersuchungen* (1884) he expresses surprise at this, because, as he says, the pollen tube here contains very little starch before fertilization. His description in Juniperus of the starch sheath appearing around the fusion nucleus immediately after its formation and the subsequent behavior of the two may be applied almost word for word to Taxodium. It seems probable, therefore, that starch may yet be found in the male cells of the Cupresseae.

The sperm nucleus before contact with the female has the same character as was noticed in the pollen tube. It is difficult to distinguish it from the protoplasm around it, but a central nucleolus and a scarce reticulum may be made out in the dense substance that completely fills the nucleus. When the sperm cell enters the egg its nucleus is not more than a fifth the diameter of the egg nucleus (*fig. 100*), but during its course to the latter the sperm nucleus enlarges somewhat (*fig. 101*), and just after contact the diameter of the two nuclei is about as one to two. The male protoplasm, with its inclosed starch, now completely infolds the egg nucleus until it becomes evenly distributed around it (*figs. 102, 103, 105*). The structure of the sperm nucleus begins to change immediately on contact with the egg nucleus. The linin substance becomes arranged into a reticulum staining deep blue with gentian, while the nucleolus seems to break up into a number of smaller granules which lie more or

less grouped, but frequently scattered in no definite position. They were not found to be definitely located near the point of contact between the two nuclei as described by Blackman ('98) and Chamberlain ('99). The fusion nucleus begins to move to the base of the archegonium, and its male and female elements can be easily distinguished until the base is nearly reached (*fig. 106*). This passing of the fusion nucleus to the base of the archegonium before division occurs has been described by Strasburger ('79, '84) in Juniperus and by Jäger ('00) in Taxus.

The partition between the two nuclei does not entirely disappear until immediately before the first division. *Fig. 119* represents the two nuclei just after the disappearance of the separating wall. The parts derived from each are still distinct, the denser part being the male. The reticulum of the sperm nucleus is arranged in a more or less radiating way, and that of the egg is also becoming thus arranged. The large plastin nucleolus of the egg nucleus may be found in all stages of fusion. In addition to the reticulum and plastin nucleolus there are also present numbers of chromatin nucleoli in each half of the nucleus. The spindle of the first division is derived entirely from the reticulum of the fusion nucleus.

The structure of the male or sperm cell of Taxodium and its behavior during fertilization are worthy of especial emphasis. The presence of large quantities of starch around its nucleus and the transfer of this starch, together with its protoplasm, to form a distinct layer around the egg nucleus, which later becomes separated from the protoplasm of the egg in the base of the archegonium to form the greater part of the young embryo, are peculiarities not as yet described in any other organism, and they seem of sufficient interest to receive attention in any comparative study of sexual cells.

All observers who have studied fertilization in the gymnosperms seem agreed that the male nucleus slips from its protoplasmic sheath as it approaches the egg nucleus and leaves it behind near the point of entrance. If the case is as they think, Taxodium is an exception here.

In his well-known work on chromatophores, leucoplasts, etc.,

A. F. W. Schimper demonstrates the presence of plastids in the egg cells of plants. Taking the occurrence of starch as an indication of the presence of leucoplasts, we find that most of the plastids of the proembryo of Taxodium are furnished by the male cell. Occasionally a few scattered starch grains may be seen in the archegonium before fertilization, but as a rule the egg protoplasm is entirely free from them at maturity. Chromatophores or leucoplasts might of course be present in the egg without the occurrence of starch, and as such bodies are rather difficult to demonstrate without special methods, their presence cannot be denied. Blackman's ('98) observation of leucoplasts in the male cell of Pinus has already been referred to.

THE EMBRYO.

Fig. 120 shows an early stage in the formation of the spindle of the first division. The reticulum has become less coarse, the larger granules seeming to become transformed into smaller ones which characterize the fibers of the spindle at this stage. The outlines of the fusion nucleus are still quite distinct, and its fibers pass into those of the spindle imperceptibly. The chromatin has become arranged on the more homogeneous fibers in the center, and form ill-defined, much-elongated bodies which are not yet grouped into a definite plate. It will be seen that the spindle is multipolar at its origin. Stages of older spindles were not found.

The plastin nucleolus derived from the egg nucleus does not disappear during the spindle formation or during division of the nucleus. It is generally inclosed in one of the daughter nuclei, but is sometimes left free in the surrounding cytoplasm. The two daughter nuclei of the first division are first separated a considerable distance (*fig. 121*), but later approach nearer and are surrounded by the same starch sheath (*fig. 117*). Their structure is very similar to that of the egg nucleus before fertilization, a plastin nucleus, a chromatin reticulum, and a large amount of finely granular linin material being present. As the fusion nucleus approaches the base of the archegonium, it may rotate so that the part derived from the sperm nucleus lies nearest the base of the archegonium (*fig. 106*). The large vacuole of the

egg becomes broken up into smaller ones as the fusion nucleus approaches it, and in some cases almost disappears; often, however, the distinct starch-containing protoplasmic sheath of the fusion nucleus or its daughter nuclei is surrounded on both sides by large vacuoles (*fig. 117*).

The two daughter nuclei of the first division very soon prepare for the second division. *Fig. 122* shows such a nucleus in an early stage of mitosis. The chromatin is arranged in distinct rods, the linin granules have formed the reticulum, and the large plastin nucleolus is conspicuous. *Fig. 123* represents a late anaphase in the spindle of the second division. The number of chromosomes is evidently greater than in the division of the central cell. At this time the distinctive protoplasm of the proembryo has filled the base of the archegonium and is becoming more and more distinct from the ordinary egg cytoplasm above it. During this division and the one following, the plastin nucleolus is frequently left outside of the daughter nuclei, and may be broken up into several parts which lie free in the cytoplasm. *Fig. 124* gives the usual arrangement of the first four nuclei of the proembryo. They lie tetrad-fashion in the base of the archegonium, and a narrow zone of disorganizing protoplasm is beginning to appear above the starch-containing sheath around them. The cytoplasm is arranged in radiating lines from the nuclei. In *fig. 126* the third division has taken place. Several plastin nucleoli are present in the cytoplasm. In *fig. 125* the four nuclei of the second division are arranged in an unusual manner. They lie in one plane at the base of the archegonium and are bounded above by a large vacuole.

Spindles of the third division do not have any definite arrangement in reference to each other or to the axis of the archegonium, but their position seems to depend a good deal upon the width of the archegonium. After the formation of the daughter nuclei, however, these become arranged as *fig. 116*. Two are situated side by side at the base, and six lie above them in one plane. While this is the usual arrangement, it is not uncommon to find only one at the base, while the other seven are arranged above it. In a few cases there were three below

and five above. An abnormal condition is shown in *fig. 128*. Here two of the eight nuclei produced by the third division have not joined in the formation of the basal group, but remain some distance above, quite separate from the proembryo beneath. Two nuclei are at the base in this case, as usual, but the number above is only four, thus making up the total eight. All these nuclei are in division. The section is somewhat oblique, so that the base of one of the upper cells is shown above the two basal cells.

After the cells are arranged as mentioned, they become separated from each other by delicate cell walls, the upper tier remaining open at the top. The fourth division now takes place almost simultaneously in all of the nuclei. The axes of the spindles in the upper tier are parallel with the axis of the archegonium (*fig. 127*). There is thus cut off from the upper cells an equal number of nuclei which lie free in the cytoplasm of the egg and form the rosette (*fig. 129*). Cell walls are produced by this division and the middle tier is now completely closed (*fig. 129*). By referring to *fig. 127* it will be seen that the starch is all grouped in the base ends of the upper tier of open cells, and that the lower poles of the spindles are imbedded in it. When walls are formed all the starch is inclosed in the middle tier with the exception of a few scattered grains in the tip cells. The spindles in the lower cells lie at right angles to the ones above, and form a tier of four cells, or of six in those cases where three original cells have been arranged at the tip, or only two where there is but one tip cell. The middle tier now elongates into the suspensors (*fig. 133*), the nuclei and most of the cytoplasm appearing at the lower end. Further division in the tip cells does not occur until the suspensors have greatly elongated.

The formation of the embryo proper shows much variation. The suspensors from a single archegonium only rarely remain completely united at their tips, but usually separate more or less. The supernumerary suspensors are left behind at various positions, so that at the time of the first division of the tip cells the number of suspensors and tip cells is usually the

same. Each tip cell divides independently of the others, even when they are near together, and different stages of development are found in embryos from the same archegonium. Generally the tip cells are separated by the spreading or unequal growth of the suspensors. *Fig. 143* shows two embryos from the same archegonium, each with its own suspensor. In *fig. 144* the embryo and suspensor shown are situated at a considerable distance from any others.

Figs. 140–142 are serial sections through a group of embryos from one archegonium. There are four in the group, only three of which are shown. It will be seen that the growth in each proceeds independently, and some of them are more advanced than others. In *fig. 139* a two-celled and a three-celled embryo are represented. The first wall is almost always inclined and produces two cells generally of unequal size. The second wall arises in the distal larger cell, and is nearly at right angles to the first. The following divisions cannot be systematized by any rule, but, as will appear from the figures, are irregularly disposed. *Fig. 135* shows a suspensor bearing two embryos on its tip. It was teased from a prothallium and mounted whole. *Fig. 136* is a more magnified view of its tip; the two embryos are proceeding each on its own course in spite of the close contact of their original walls. In *fig. 146* the more advanced embryo seems to be formed of three distinct parts which may be interpreted as derived from three separate tip cells which proceeded alone in their development for a time, but being closely associated have united to form a single embryo. In *fig. 145* a single suspensor bears a single embryo. The embryonal tubes have appeared, but are not quite so much developed as in *fig. 146*. In *fig. 147* is shown the most advanced stage obtained of the young embryo. The embryonal tubes are very numerous and extend about four times farther up than is shown in the figure. They have completely filled the space previously occupied by the suspensor, of which no trace can be seen at this time. Three abnormal embryos are shown in *figs. 130–132*.

From this description it will be seen that the development of the embryo of Taxodium differs from all other conifers. In

Taxus (Jäger, '99) and Cephalotaxus (Arnoldi, '00) there are more than eight free nuclei present before cell formation, and the tiers are not so definite as in Taxodium. In the Cupresseae (Strasburger, '72) the tiers are at first composed of single cells, while in the Abieteae only one tier is first formed which then gives rise to four by successive divisions. Coulter ('97) and Coulter and Chamberlain ('01) have described peculiarities in the number of embryos formed from one archegonium, and in the relation of suspensors to embryos in *Pinus Laricio*, which are not unlike the diversities found in Taxodium.

SYSTEMATIC POSITION OF TAXODIUM.

The family Taxodieae as arranged by Eichler is acknowledged a tentative one, and when we compare the gametophytes of Sequoia and Taxodium, the only two genera of this family in which this part of the life history has been followed, we are impressed, not with similarities, but with divergencies; and it becomes at once apparent that, if gametophytic characters are of any consequence in classification, the group as it now stands is an artificial one and must be rearranged. The points of divergence between Taxodium and Sequoia are so striking that to retain them longer in the same group would do violence to taxonomic principles. In the large number of functional megaspores and prothallia present in its sporangia Sequoia is markedly primitive, and in the arrangement and number of its archegonia it is, so far as known, *sui generis*. Its male gametophyte is imperfectly known, the young stages being quite unstudied.

In the preceding pages attention has been called in passing to certain of the more evident structural similarities between Taxodium and the Cupresseae, and for the sake of brevity they will not again be rehearsed here. It is sufficient to say that Taxodium agrees with the Cupresseae in all gametophytic characters that seem to me of much taxonomic importance, and I think it evident that such essential agreement with the Cupresseae on the one hand and such fundamental divergence from Sequoia on the other must necessitate the removal of Taxodium from its connection with the latter and its insertion in the former family.

Such a change will require us to discard the name Taxodieae and combine the remaining genera of the family into some tentative group of another name until further study shall make their position clear.

SUMMARY.

The staminate cones begin to develop in September or October, and by winter the pollen mother-cells are formed. In spring starch is removed from the cells of the sporophyll and stored in the mother-cells, where it remains through their divisions and disappears in the pollen grain as the exine is being formed. The exposed wall of the microsporophyll is but two layers thick.

The reducing divisions in the pollen mother-cells resemble those in the Larix and the reduced number of chromosomes is probably twelve. There is a fairly well developed resting stage after the first division in the mother-cells.

About ten days after the reducing division a division of the pollen grain occurs which separates at once the generative cell from the tube cell. No sterile prothallial cells are formed.

From two to three weeks after pollination, when the pollen tube has grown some distance, the generative cell divides into the central cell and stalk cell, and these move down toward the tube nucleus. The pollen tube reaches the prothallium earlier than in any case previously described, sometimes even before the formation of a cellular tissue in the latter.

The arrangement of the nuclei in the pollen tube is the same as in other conifers.

The central cell has a distinct *Hautschicht* of its own and resembles in outline that of Taxus and the Cupresseae. It divides simultaneously with the division in the central cell of the archegonium, and the two sperm cells thus formed move apart slightly. They are furnished with a dense layer of starch around the nucleus, a peripheral finely granular layer often containing globules of plastic material, and a *Hautschicht*. Its nucleus is densely filled with granular material and has a coarse chromatin recticulum and a nucleolus.

The ovulate cones also begin their development in early fall and continue growing slowly, as the weather permits, through

the winter. At the time of pollination the single megaspore mother-cell may be distinguished. It is filled with starch, as are also the tapetal cells around it. Two reducing divisions occur, but only three cells are formed, the upper of the two first produced not dividing again. The lower of the two potential megaspores resulting from the second division in the lower cell develops into the female gametophyte, the two upper cells disorganizing.

As the spore develops in sprouting, the tapetal cells around it grow and divide, and disorganizing the nucellar cells around them pass the nourishment to the prothallium within. How long this tapetum persists is not certain, but it probably lasts until the prothallium is mature.

The archegonia are arranged as in the Cupresseae. The number of the neck cells vary from two to sixteen or more. The central cell is very long and contains two conspicuous kinoplasmic areas, one at the upper end near the nucleus and the other in the lower end beneath the large central vacuole. When the ventral canal nucleus is cut off the upper of these masses takes part in the division, while the fragmented lower one fills the base of the archegonium with peculiar figures.

A ventral canal nucleus is cut off just before fertilization, but it is not separated from the cytoplasm of the egg and after fertilization moves back toward the center and divides amitotically. It probably assists in nourishing the embryo.

The spindle of the ventral canal cell division is almost entirely of nuclear origin, and the chromosomes are derived largely from the nucleolus. The egg nucleus contains a large amount of granular material, but a chromatin reticulum is always present. This granular material is largely used in the formation of the spindle of the fusion nucleus.

Fertilization occurs about the middle of June, and two or more sperm cells may enter an archegonium. Only one, however, becomes fused with the egg cytoplasm. As a rule one pollen tube fertilizes two archegonia.

The sperm cell with its starch, protoplasm, and nucleus passes through the cytoplasm of the tip of the egg and reach-

ing the female nucleus enfolds it. Its starch is uniformly distributed around the fusion nucleus and passes with it to the base of the archegonia to be included in the cytoplasm segregated off as the proembryo. The larger part of the cytoplasm of the egg takes no direct part in the formation of the embryo, but is digested and used by the latter in its growth.

The first division occurs after the fusion nucleus has reached the base of the archegonium.

Eight free nuclei are formed, which arrange themselves in two tiers, the upper of which generally contains six, the lower two. Cell walls are now formed, but the upper side of the upper tier is left open. This open tier now divides by walls at right angles to the long axis of the archegonium into the rosette of free nuclei above and the suspensors below. The two cells of the lower tier divide at the same time by walls parallel to the long axis of the archegonium, and thus four cells instead of two are produced in one plane.

The suspensors as they elongate may or may not separate, and thus one or several embryos may be formed from one archegonium.

It is thought that the family Taxodieae as now composed is an artificial one; that Taxodium itself must be removed to the Cupresseae, leaving Sequoia and perhaps other as yet imperfectly known genera of the present family Taxodieae to be included in a family of their own under another name.

NOTE.

Since the completion of this work in May, 1901, several papers have appeared bearing more or less closely on certain points here taken up. Miss Ferguson's two papers on fertilization, etc., in Pinus (Annals of Botany, 1901), and Arnoldi's *Beiträge zur Morph. de Gymn.* V. (Bull. Soc. Imp. Nat. Moscow, No. 4, 1900), dealing with fertilization, embryo formation, etc., in the "Sequoiaceen," are important, and would have been referred to frequently in the text had they appeared before this work was handed in. Miss Ferguson confirms Blackman's ('98) statement that the sperm cells of Pinus are furnished with a cyto-

plasm of their own, though the outline of the cell seems to be neither so regular in shape nor so definite in outline as in other groups of gymnosperms. She finds no starch in the male cells, although much is present in the pollen tube. Miss Ferguson also suggests that the "spongy" tissue is useful in nourishing the prothallium, and brings out other interesting points, which must, however, be passed by here.

Arnoldi, in the communication mentioned, finds starch in the sperm cells of Sequoia, Cryptomeria, and Taxodium, and notes its transference to the embryo. He also considers necessary the removal of Taxodium (and several other genera) into the Cupresseae; but on certain points of fact in developmental processes our work does not agree.

In the recent Belfast meeting of the British Association Mr. Harold Wager presented a paper on the function of the nucleolus, in which he is reported as finding that "this body, in the cases examined by him, appears to be intimately connected with the nuclear network, and contains chromatin material which contributes directly to the formation of the chromosomes" (Nature **67**: 20. 1902). These results are of interest in connection with my conclusions.

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LITERATURE CITED.

ARNOLDI, W., '99[a]: Beiträge zur Morphologie der Gymnospermen. I. Bull. Soc. Nat. Moscow **14**: 329–341. *pls. 7–8.* 1899.

——— '99[b]: Beiträge zur Morphologie der Gymnospermen. II. Bull. Soc. Nat. Moscow **14**: 405–422. *pls. 10–11.* 1899.

——— '00: Beiträge zur Morphologie der Gymnospermen. III. Flora **87**: 46–63. *pls. 1–3.* 1900.

——— '00: Beiträge zur Morphologie der Gymnospermen. IV. Flora **87**: 194–204. *pls. 6–7.* 1900.

BELAJEFF, W., '91: Zur Lehre von dem Pollenschlauche der Gymnospermen. Ber. Deutsch. Bot. Gesell. **9**: 280–286. *pl. 18.* 1891.

——— '93: Zur Lehre von dem Pollenschlauche der Gymnospermen. Ber. Deutsch. Bot. Gesell. **11**: 196–201. *pl. 12.* 1893.

BLACKMAN, H., '98: On the cytological features of fertilization and related phenomena in *Pinus sylvestris*. Trans. Roy. Soc. **190**: 395–426. *pls. 12–14.* 1898.

CHAMBERLAIN, C. J., '98: Winter characters of certain sporangia. BOT. GAZ. **25**: 125–128. *pl. 11.* 1898.

——— '99: Oogenesis in *Pinus Laricio;* with remarks on fertilization and embryology. BOT. GAZ. **27**: 268–280. *pls. 4–6.* 1899.

COULTER, J. M., '97: Notes on the fertilization and embryogeny of conifers. BOT. GAZ. **23**: 40–43. *pl. 6.* 1897.

——— and CHAMBERLAIN, C. J., '01: Morphology of Spermatophytes. Part I. Gymnosperms. New York, 1901.

DAVIS, B. M., '98: Kerntheilung in der Tetrasporen-mutterzelle bei *Corallina officinalis* L. var. *Mediterranea.* Ber. Deutsch. Bot. Gesell. **16**: 266–272. *pls. 16–17.* 1898.

DIXON, H. H., '94: Fertilization of *Pinus sylvestris.* Ann. Botany **8**: 21–34. *pls. 3–5.* 1894.

DUGGAR, B. M., '99: On the development of the pollen grain and the embryo-sac in *Bignonia venusta.* Bull. Torr. Bot. Club **26**: 89–105. *pls. 352–354.* 1899.

FARMER, J. B., '92: Occurrence of two prothallia in ovule of *Pinus sylvestris.* Ann. Botany **6**: 213, *fig. 1.* 1892.

GARDINER, W., '83: On the continuity of the protoplasm through the walls of vegetable cells. Phil. Trans. Roy. Soc. London **35**: 163–166. 1883.

GOROSCHANKIN, J., '83: Zur Kentniss der Corpuscula bei den Gymnospermen. Bot. Zeit. **41**: 825–831. *pl. 7A.* 1883.

HIRASÉ, S., '95: Étude sur la fécondation at l'embryogénie du *Ginkgo biloba.* Jour. Coll. Sci. Imp. Univ. Tokio **8**: 307–322. *pls. 31–32.* 1895.

HOFMEISTER, W., '51: Vergleichende Untersuchungen. 1851.

IKENO, S., '98: Untersuchungen über die Entwickelung der Geschlechtsorgane und der Vorgäng der Befruchtung bei *Cycas revoluta.* Jahrb. Wiss. Bot. **32**: 557–602. *pls. 8–10.* 1898.

——— '01: Contribution à l'étude de la fécondation chez le *Ginkgo biloba.* Ann. Sci. Nat. Bot. **13**: 305–318. *pls. 2–3.* 1901.

JÄGER, L., '99: Beiträge zur Kenntniss der Endospermbildung und zur Embryologie von *Taxus baccata* L. Flora **86**: 241–288. *pls. 15–19.* 1899.

JUEL, H. O., '00: Beiträge zur Kenntniss der Tetradentheilung. Jahrb. Wiss. Bot. **35**: 626–659. *pls. 15–16.* 1900.

JURANYI, L., '82: Beiträge zur Kenntniss der Pollen-Entwickelung der Cycadeen and Coniferen. Bot. Zeit. **40**: 814–818, 835–844. 1882.

MURRILL, W. A., '00: The development of the archegonium and fertilization in the hemlock spruce (*Tsuga canadensis*). Ann. Botany **14**: 583–607. *pls. 31–32.* 1900.

MITZKEWITSCH, L., '98: Ueber die Kerntheilung bei Spirogyra. Flora **85**: 81–124. *pl. 5.* 1898.

SHAW, W. R., '96: Contribution to the life history of Sequoia. BOT. GAZ. **21**: 332–339. *pl. 24.* 1896.

SOKOLOWA, MLLE. C., '90: Naissance de l'endosperme dans le sac embryonnaire de quelques Gymnospermes. Bull. Soc. Nat. Moscow. *pl. 2.* 1890.

STRASBURGER, E., '72: Die Coniferen und die Gnetaceen. 1872.

——— '77: Die Befruchtung und Zelltheilung. Jenaisch. Zeitsch. **2**: 435–536. *pls. 27–35.* 1877.

——— '79: Die Angiospermen und die Gymnospermen. 1879.

——— '84: Neue Untersuchungen, etc., 1884.

——— '92: Ueber das Verhalten des Pollens und die Befruchtungsvorgänge bei den Gymnospermen. Hist. Beitr. **4**: 1–158. *pls. 1–3.* 1892.

——— '00: Ueber Reduktionstheilung, etc. Hist. Beitr. **6**: 1900.

WEBBER, H. J., '97[a]: Peculiar structures occurring in the pollen tubes of Zamia. BOT. GAZ. **23**: 453–459. *pl. 40.* 1897.

——— '97[b]: The development of the antherozoids of Zamia. Bot. Gaz. **24**: 16–22. 1897.

——— '97[c]: Notes on the fecundation of Zamia and the pollen tube apparatus of Ginkgo. BOT. GAZ. **24**: 225–235. *pl. 10.* 1897.

EXPLANATION OF PLATES I–XI.

The abreviations used are: *st*, stalk cell or stalk cell nucleus; *gr*, generative cell; *ptn*, pollen tube nucleus; *cc*, central cell of pollen tube; *scl*, sclerenchymatous cells; *vcn*, ventral canal nucleus; *en*, egg nucleus.

PLATE I.

FIG. 1. Median longitudinal section through young microsporangium; primary archesporium evident as rows of cells. × 400.

FIG. 2. Microsporangium in October; tapetum differentiated. × 300.

FIG. 3. Spindle of first division of microspore mother cell. × 800.

FIG. 4. Anaphase of same, showing four limbs to chromosomes. × 800

FIGS. 5–6. Chromosomes seen from poles as they approach them; eleven in *fig. 11*. × 800.

FIG. 7. Spindle of second division; mother-cell walls not yet dissolved. × 800.

FIG. 8. Microspore before first division; cell wall not shown. × 800.

FIGS. 9–11. Successive stages in first division of microspore. × 800.

FIG. 12. Pollen grain on tip of nucellus, exine split off. × 800.

FIG. 13. Pollen grain beginning to germinate, exine split off and generative cell swelling out. × 800.

FIG. 14. The same; young stage of germination. × 500.

FIG. 15. Tube nucleus moving down. × 500.

FIG. 16. Different relative position of generative cell and pollen tube than in above. × 500.

FIG. 17. Indication of branching in pollen tube. × 500.

FIG. 18. Generative cell just before commencing to divide. × 800.

FIG. 19. Generative cell immediately after division. × 800.

FIG. 20. Pollen tube with three nuclei. × 280.

FIG. 21. Central and stalk cell of same tube more magnified; stalk cell protoplasm beginning to merge into that of pollen tube. × 800.

FIG. 22. All three nuclei moving down, and close together. × 400.

FIG. 23. Pollen tube slightly older; stalk nucleus has passed central cell and lies by tube nucleus from which it differs in its smaller size; May 15, 1900. × 400.

PLATE II.

FIG. 24. More developed pollen tube; stalk and tube nuclei alike. × 235.

FIG. 25. Tip of ovule; pollen tube has reached megaspore in which no cell walls have yet formed. × 26.

FIG. 26. Tip of pollen tube that has reached the prothallium; nuclei in usual position. × 400.

FIG. 27. Central cell of pollen tube shortly before division; one free nucleus shown. × 800.

FIG. 28. Central cell preparing to divide; free nuclei and protoplasm of pollen tube disorganizing. × 400.

FIG. 29. Spindle of division of central cell. × 800.

FIG. 30. Telophase of the same. × 400.

FIG. 31. Sperm cells separated from each other. × 400.

PLATE III.

FIG. 32. Megasporophyll with the axillary megasporangium rudiment just beginning to show; Oct. 3, 1899. × 95.

FIG. 33. The same; integument beginning to appear; Jan. 4, 1900. × 95.

FIG. 34. Little older megasporophyll and ovule; March 11, 1900, Baltimore. × 95.

FIG. 35. The same; ready for pollination; megaspore mother-cell not yet divided; March 31, 1900. × 80.

FIG. 36. Longitudinal section of sporangia and sporophyll ten days after pollination; placenta now beginning to appear above the ovule; April 3, 1901. × 36.

FIG. 37. Sporophyll and ovule about three weeks after pollination; micropyle closed and placenta becoming prominent; April 22, 1900. × 36.

FIG. 38. Megaspore mother-cell before division. × 800.

FIG. 39. The same; in synapsis. × 1030.

FIG. 40. The same; spindle of first division. × 950.

FIG. 41. The same; older spindle of first division. × 950.

FIG. 42. The same; wall being formed. × 950.

FIG. 43. The same; spindle of second division. × 950.

FIG. 44. Megaspore with the two disorganizing spores above. × 950.

PLATE IV.

FIG. 45. Megaspore before first division; distinct zone of large cells around it. × 400.

FIG. 46. Two cells of the large-celled tissue in division. × 800.

FIG. 47. Germinating megaspore in middle of large-celled tissue; April 29, 1900. × 70.

FIG. 48. Enlarged section of the above-mentioned tissue. × 400.

FIG. 49. Longitudinal section of entire ovule five weeks after pollination. × 36.

FIG. 50. Ovule showing two prothallia. × 70.

FIG. 51. Longitudinal section showing nucleated cytoplasm of wall layer of megaspore, large-celled tissue, and nucellus cells. × 400.

FIG. 52. Large-celled layer around somewhat older prothallium. × 280.

FIG. 53. The same; after-formation of prothallial cells. × 280.

FIG. 54. Young stage, ingrowing cells of prothallium. × 280.

PLATE V.

FIG. 55. Prothallial tubes, after closure of inner ends. × 280.

FIG. 56. Two-celled stage of the same. × 280.

FIG. 57. Tip of young prothallium showing group of archegonium initial cells. × 70.

FIG. 58. Prothallial cell becoming multinucleate. × 400.

FIG. 59. The same with five nuclei. × 400.

FIG. 60. Formation of neck cells in archegonia. × 280.

FIG. 61. Older archegonium; neck cell divided. × 280.

FIG. 62. Still older archegonium; kinoplasmic areas beginning to appear. × 280.

FIG. 63. Nucleus of central cell of archegonium at same age as above. × 400.

FIG. 64. Group of archegonia showing ten in one section, two pollen tubes above; somewhat diagrammatic. × 70.

FIG. 65. Cross-section of group of archegonia, showing seventeen. × 85.

PLATE VI.

FIG. 66. Archegonium showing kinoplasmic masses in central cell; after entrance of plastic stuff from neck cells. × 280.

FIGS. 67–69. Jacket cells in normal activity. × 800.

FIG. 70. Spindle in jacket cell at time of fertilization. × 800.

FIGS. 71–74. Stages of disintegration of nuclei of jacket cells. × 800.

FIG. 75. Lower part of archegonium at time of fertilization showing proteid vacuoles. × 800.

FIGS. 76–82. Successive stages in division of central cell of archegonium; *fig. 76.* × 400; *figs. 77–82.* × 800.

PLATE VII.

FIGS. 83–90. Successive stages in division of central cell of archegonium; *figs. 83–89.* × 800; *fig. 90.* × 280.

FIG. 91. Group of archegonia after formation of ventral canal nuclei. × 36.

FIG. 92. Two archegonia of same group slightly more magnified. × 70.

FIGS. 93–96. Neck cells seen from above. × 400.

FIGS. 97–98. Surface view of megaspore wall showing pits; after formation of young prothallium. × 800.

FIG. 99. Pits of same wall in section. × 800.

PLATE VIII.

FIG. 100. Sperm cell just entering cytoplasm of archegonium tip; its nucleus barely visible in dense starch sheath around it. × 800.

FIG. 101. Sperm cell protoplasm just touching egg nucleus; sperm nucleus not yet in contact with egg nucleus. × 800.

FIG. 102. Sexual nuclei in contact; sperm cell protoplasm beginning to inclose the egg nucleus. × 400.

FIG. 103. Later stage of fusion. × 400.

FIG. 104. Supernumerary sperm cell in tip of archegonium. × 400.

FIG. 105. Later stage of fusion; starch sheath completely inclosing the not yet entirely fused nuclei. × 400.

FIG. 106. Archegonium at the stage above; fusing nuclei moving down and large vacuole broken up. × 70.

FIG. 107. Egg and ventral canal nucleus in tip of an archegonium that did not get fertilized. × 280.

FIG. 108. Ventral canal nucleus at tip of an archegonium of same group as above which has been fertilized and has a two-celled embryo in the base. × 280.

FIG. 109. Ventral canal nucleus in another fertilized archegonium of same group; it has grown out into the protoplasm and is beginning to divide amitotically. × 280.

FIGS. 110–112. Successive stages in growth of ventral canal nucleus in fertilized archegonia; all with young embryos in base; extra sperm cell lying in tip of archegonium in 110. × 400.

PLATE IX.

FIGS. 113–114. Ventral canal cells in archegonia that missed fertilization; others in group have been fertilized. × 280.

FIG. 115. Amitotic division of ventral canal nucleus. × 400.

FIG. 116. Archegonium with 8-celled embryo at base; wells are formed between the cells, but upper cells open above; here there are seven cells in upper tier and only one below; canal nucleus at tip; disorganized layer above embryo. × 400.

FIG. 117. Archegonium with two-celled embryo near base; ventral canal nucleus in division above, and second sperm cell free in tip. × 280.

FIG. 118. Ventral canal nucleus divided, lying at base of archegonium in contact with two-celled embryo, only one of the nuclei of which is shown; embryo surrounded by its starch sheath. × 400.

FIG. 119. Late stage of fusion of sperm and egg nuclei. × 800.

FIG. 120. Spindle of first division of fusion nucleus; large plastin nucleolus unchanged. × 800.

FIG. 121. Two daughter nuclei of fusion nucleus, immediately after division. × 800.

FIG. 122. Preparation for second division. × 400.

FIG. 123. Spindle of second division. × 800.

PLATE X.

FIG. 124. Four-celled embryo; nuclei in usual position, two above and two below arranged tetrad fashion. × 280.

FIG. 125. Embryo of same stage as above, nuclei all arranged at base in one plane. × 280.

FIG. 126. Spindles of third division; plastin nuclei in protoplasm. × 280.

FIG. 127. Eight-celled embryo, six cells above and two below; the upper are dividing, the lower preparing to divide. × 280.

FIG. 128. Abnormal embryo, cut a little obliquely; two of the nuclei have not joined in the tier formation, but have remained a little distance above, and in dividing only one is shown; the other lies beside it in another section. × 280.

FIG. 129. Sixteen-celled embryo in three tiers; six cells in rosette, six suspensor cells, and four below. × 280.

FIGS. 130–132. Abnormal embryos. × 280.

FIG. 133. Sixteen-celled embryo after suspensors have lengthened considerably. × 280.

FIG. 134. Cross-section through a group of seven suspensors. × 400.

FIG. 135. A single suspensor carrying two embryos which are developing separately. × 29.

FIG. 136. Tip of above suspensor with its two embryos more magnified. × 400.

FIG. 137. A two-celled and a three-celled embryo, each on its own suspensor. × 280.

PLATE XI.

FIG. 138. Two four-celled embryos; there are four embryos in the group and four suspensors; three of the embryos are four-celled, and one about six-celled. × 280.

FIG. 139. A three-celled and an about eight-celled embryo; four embryos in group and three suspensors. × 280.

FIGS. 140–142. Three consecutive sections through a group of four

embryos hung by three suspensors; the fourth embryo does not appear in these sections. × 280.

FIG. 143. Two embryos, each on its own suspensor; they are from the same archegonium; there are two others in the group. × 280.

FIG. 144. One embryo on one suspensor, off to itself. × 280.

FIG. 145. Older embryo on much enlarged tip of suspensor; embryonal tubes beginning to appear. × 280.

FIG. 146. Apparently three embryos of a group uniting to form a single embryo; embryonal tubes conspicuous. × 280.

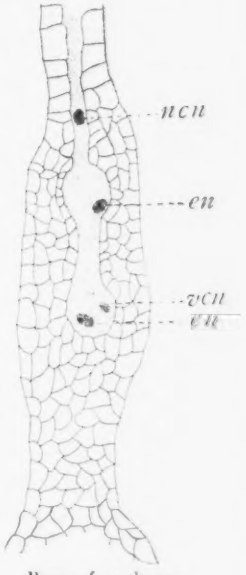
FIG. 147. Older embryo; embryonal tubes extend up about four times as far as shown. × 280.

BRIEFER ARTICLES.

THE OCCURRENCE OF TWO VENTERS IN THE ARCHEGONIUM OF POLYTRICHUM JUNIPERINUM.

THE interesting phenomenon of a double venter in the archegonium of *Polytrichum juniperinum* was observed, in material sectioned and studied by the writer, in a course of comparative morphology and embryology of plants under the direction of Dr. Margaret C. Ferguson, of Wellesley College.

The archegonium illustrated in the accompanying figure shows two distinct venters, the lower venter containing two nuclei, which probably represent the egg cell and the ventral canal cell. The upper venter has doubtless been developed from the first neck canal cell and contains but a single nucleus. Directly above, in the neck of the archegonium, is the nucleus of the second neck canal cell.



Base of archegonium of *Polytrichum juniperinum* showing two venters.

Previous to the time that these observations were made, no similar phenomenon had been noted as occurring in the archegonium of the Musci, but, while preparing this note for publication, the February number of the BOTANICAL GAZETTE appeared, in which the "occurrence of two egg cells in the archegonium of Mnium" was described by Coker.[1]

There are two opinions held today regarding the origin of the neck canal cells. According to Campbell,[2] the neck canal cells are derived from the terminal cell cut off from the mother-cell of the archegonium, while Gayet[3] maintains that, in the Musci as in the Hepaticae, the terminal cell does not give rise to the neck canal cells, but that

[1] COKER, W. C., On the occurrence of two egg cells in the archegonium of Mnium. BOT. GAZ. **35**: 136. 1903.

[2] CAMPBELL, D. H., Mosses and ferns 194. 1895.

[3] GAYET, L. A., Recherches sur le développement de l'archegone chez les Muscinées. Ann. Sci. Nat. Bot. VIII. **3**: 161–258. 1897.

they are derived from an initial cell cut off from the mother-cell of the oosphere. It would seem from the recent observations of two egg cells in the archegonium of Mnium and of Polytrichum that the neck canal cells are potential egg cells, and as such argue for Gayet's theory that the egg cell and neck canal cells have a common origin.— MARY C. BLISS, *Wellesley College.*

POLYEMBRYONY IN GINKGO.

IN the BOTANICAL GAZETTE **34**: 64, July 1902, I published a short note on the polyembryony of Ginkgo. Since polyembryony is of rather common occurrence among the gymnosperms, its frequency in Ginkgo becomes a point of some interest. Through the kindness of Dr. George T. Moore and Mr. Carl Kellerman, of the Department of Agriculture, I have secured a number of seeds of the Ginkgo. A careful examination of two hundred specimens give the following results: 12 per cent. were without embryos, while 2 per cent. showed two small but well-formed embryos in each seed. In the cases of polyembryony the embryos averaged about one-third the length of the single embryos. With one exception, the double embryos were approximately the same length; in this case one embryo was about twice the length of its fellow. The single embryos showed great variation in length, but the short ones were always thicker than the long ones. One embryo had three well-developed cotyledons. — MEL. T. COOK, *De Pauw University, Greencastle, Ind.*

CURRENT LITERATURE.

BOOK REVIEWS.

Plant physiology.

PROFESSOR G. J. PEIRCE, of Stanford University, has elaborated lectures upon plant physiology which he has been giving in the University into a text-book,[1] less extensive than Pfeffer's treatise, and more full than Noll's treatment in the Bonn text-book. This is published in attractive form and will be found of interest both to the general reader and to students. The book differs from the *Text-book of plant physiology* by MacDougal, in that there are no laboratory directions, the author believing that the laboratory manual and the text should be divorced. The only English work with which the book at all competes is the *Vegetable physioiogy* of Professor J. Reynolds Green.

Peirce's book shows strongly the impress of Pfeffer's *Physiology*, and to him the author makes ample acknowledgment. One who reads the book carefully will be impressed by the clearness of style and the vigor of presentation, as well as by the freshness of much of the matter and the modern point of view from which the author regards his subject. The book is characterized by two features: first, an endeavor to state the phenomena of plant life in the terms of physics and chemistry; and, second, by the clear recognition of the fact that very many plant phenomena cannot yet be adequately stated in these terms, and the consequent acknowledgment that they are at present not sufficiently known. This makes the book stimulating to the student, for many lines along which research will be profitable are pointed out to him. In many ways the book is a decided advance upon any English text which has come to our notice.

After recognizing fully the value of this work, its originality, its vigor, its clearness, its stimulating statements of the incompleteness in our knowledge, and its probable marked usefulness as a text-book in colleges and schools, there remains the less pleasant task of pointing out some of its shortcomings.

After an introductory chapter, the first topic is respiration, and here we think the author has adopted an unfortunate theory which does not agree with the observed phenomena. The whole treatment is based upon the theory that foods of various kinds are directly oxidized to furnish energy. This is plainly derived from Pfeffer, and of course should be stated as a theory; but the other view of respiration, which, in our judgment, is much more probable because in closer harmony with the facts, is not even mentioned.

In the chapter on nutrition which follows, there is no adequate treatment

[1] PEIRCE, GEORGE JAMES, A text-book of plant physiology, 8vo. pp. vi + 291. *figs. 22.* New York: Henry Holt and Company. 1903. $2.00.

of the mode of absorption of gases, which is repeatedly spoken of as though it were merely their diffusion from the external air into the intercellular spaces.

We are glad that Professor Peirce adopts the view that the food of all plants consists of complex carbon compounds; but he does not always in his terminology distinguish between foods and the materials out of which green plants may construct foods. Assimilation is very properly distinguished from photosynthesis. The treatment of the latter might have been somewhat extended with profit. It would have been especially desirable to include some notice of the work of Friedel (1901) on extracellular photosynthesis, especially as that work was confirmed in the autumn of 1902 by Macchiati.

It would seem that the chapter on absorption and movement of water might have been advantageously placed at the beginning of the book, since such processes are fundamental to an understanding of respiration or nutrition. The discussion of absorption, transfer, secretion, etc., are in the main clear and in accordance with modern physical notions, though there are some slips that should be corrected in later editions, such as the definition of osmotic pressure. In the treatment of transpiration and the movement of gases, however, the author has not freed himself from older and untenable ideas. This is well illustrated by the sentence: "It may easily happen in temperate regions that the plant takes in more water and more salts than it really needs, and that while the former evaporates, the latter accumulate in useless forms and quantities, with or without chemical change." Similarly, the account of gas exchanges in the intercellular spaces is open to serious criticism.

We fear that readers will be somewhat puzzled in the chapter on growth by such contradictory statements as these: "Growth is a process dependent upon the formation of new protoplasm" (p. 165); "The second stage in growth . . . . consists mainly, if not wholly, in the absorption of water" (p. 167). On page 166 we have the formation of new protoplasm and new cells described as "the first and *fundamental* stage in the process of growth;" while on page 174 we are told, "Cell division . . . . does not constitute an essential part of the process of growth."

The treatment of the subject of irritability is distinctly novel and interesting. For the student, however, it lacks a logical presentation of the phenomena of irritability which are common to all its manifestations. The chapter on reproduction, which in many physiological books is merely an account of the morphological phenomena, is noteworthy in being almost purely physiological, and it makes very obvious how little we yet know about the physiology of reproduction. In this connection the author lays more stress upon the results of Klebs than future study is likely to justify, since Klebs omitted all consideration of the effects of osmotic pressure in the solutions with which he was working. It is not unlikely, therefore, that his conclusions will be profoundly modified when this factor is taken into account. Certainly the work of Livingston, Greeley, and others, points strongly in this direction.

That the topic digestion is nowhere treated is certainly a noteworthy omis-

sion. Only as an incident in the chapter on nutrition is it mentioned that foods temporarily stored in the chloroplasts must be transformed before removal, and implications of the same kind occur in connection with the general subject of the transfer of foods. But nowhere is there any discussion of the important part which digestion plays in plant life, nor any account of the agents by which it is accomplished.

It would not be difficult to point out minor inaccuracies here and there in Professor Peirce's book, nor unfortunate modes of expression; an illustration of the latter, and one very common in physiological writings, is repeated many times when he speaks of natural "laws" as though they were objective and efficient agents.

Professor Peirce's book contains so many excellent features that it is unfortunate to have it marred somewhat by sins of omission and commission. But all these matters may be rectified in future editions without fundamentally changing the character of the book, which will be useful to students, particularly if they have access to other books; and nowadays no student ought to get his physiological information from one source.—C. R. B.

Diffusion and osmotic pressure.

The rôle of diffusion and osmotic pressure in plants, by Dr. Livingston, is a well-made and attractive-looking volume of 149 pages, constituting one of the Decennial Publications of the University of Chicago.[2]

For several years the need of a concise, yet sufficiently detailed, statement of the facts and modern theories of diffusion and osmosis, on both the physical and the physiological side, has been felt by every student and teacher of physiology. Such a volume has now appeared.

Dr. Livingston has divided his book into two parts, one dealing with physical and the other with physiological considerations. In the first part we have Matter and its states, Diffusion and diffusion tension, Liquid solutions, Ionization, Osmotic phenomena, Measurement and calculation of osmotic pressure; and in the second part Turgidity, Absorption and transmission of water, Absorption and transmission of solutes, Influence of the osmotic pressure of the surrounding medium upon organisms.

After stating briefly the theories of matter, the author proceeds to the consideration of the diffusion of gases, liquids, and solids, and then in the following chapter discusses in a lucid manner the difficult subject of solutions, using this opportunity to repeat and apply the teachings of the preceding chapter on diffusion, and showing his regard for the needs of the student by defining such terms as *normal solution*, *gram-molecule solution*, and *gram-equivalent* solution.

[2] LIVINGSTON, BURTON E., The rôle of diffusion and osmotic pressure in plants. Decennial Publications of the University of Chicago, Second Series, Vol. VIII. 8vo. pp. xvi + 149. University of Chicago Press. 1903. $1.50.

A brief discussion of the ionization of gases and of solutes in solution opens the way for a very satisfactory presentation of the general subject of osmosis, wherein the osmotic pressure of non-electrolytes, electrolytes and colloids is treated, and the means and methods of measuring and calculating the pressure are set forth with appropriate formulas.

Having laid a foundation in the physical, the author proceeds to the still more difficult physiological. To this part nearly a hundred pages are given. Only a few of the more striking topics can be mentioned here. Plasmolysis is shown to be not a matter of simple interpretation, as one would infer from literature generally, but a thing to be judged only after the permeability of the protoplasmic membrane is known. To determine the permeability various tests are detailed. The action of the protoplasmic membrane and the maintenance of turgidity in spite of permeability are two of the most interesting because most difficult theoretical discussions. It is evident that the author inclines to the solvent theory as applied to the action of the membrane in osmosis. In the chapters on the absorption and transmission of water and solutes, the means of lifting the sap to the tops of trees, and the means of èxudation from water-pores, nectaries, etc., receive due consideration. These most difficult questions are not, as is too often the case, dismissed with the statement that there are no satisfactory explanations, but carefully and clearly the principal experimental results are recorded, their bearing pointed out, and their insufficiency noted. The pumping action of osmosis and the tensile strength of water are given as both probable means in the lifting of sap to great heights; while a change in the permeability of the protoplasmic sac is given as the possible cause of the beginning of excretion by water-pores and nectaries.

The last chapter represents in large measure original work by the author. Here are summarized his well-known experiments on the morphology of algae as influenced by the osmotic pressure of the surrounding medium. The work of Loeb, Massart, Rothert, and others, on the effect of osmotic pressure on irritability and in inducing parthenogenesis finds appropriate mention.

In the book as a whole there is little to criticise adversely and much to praise. Possibly the author pushes the theoretical a little too far sometimes, as, for example, in his explanation of the rise of a solution in a thistle-tube used as an osmometer. But it is better to state an insufficient hypothesis than to ignore all. In the reviewer's opinion one of the merits of the book is its abundance of theories clearly and boldly stated, while at the same time it points out the strength and weakness of each.

Pedagogically the treatment is excellent. The parts are well arranged, everything is interesting, a basis for the physiological is laid in the physical, there are copious citations of literature, and there are many suggestions as to problems for research. In the opinion of the reviewer Dr. Livingston has produced an excellent treatise.—FREDERICK C. NEWCOMBE.

White rot.

IN A SUMPTUOUS VOLUME of 300 pages, embellished by 24 elegant double colored plates, the Hungarian Department of Agriculture has published a detailed account of Dr. Gy. de Istvánffi's studies on the white rot of the grape (*Coniothyrium Diplodiella*).[3] The first part of the work is devoted to a minute description of the development of the disease, and the reactions induced in the host plant by the fungus. Of the latter the author distinguished four stages or degrees of injury occurring on the stems of American vines. The most interesting of these is the phenomenon termed "complete girdling" which is described at great length. The results produced are similar to the effects of artificial girdling. Further, the results of studies of the fungus in cultures and of artificial infections are described.

The most interesting part of the work is that which deals with the effects of various toxic substances on the fungus. A few examples are briefly given here. Vigorous mycelium from pure cultures was not injured by being immersed for 24 hours in a 2 per cent. copper sulfate solution, or in Bordeaux mixture made of 2 per cent. copper sulfate and 2 per cent. lime. When again transferred to nutrient solution the mycelium developed fruit in 18 to 20 days. On the other hand 2 per cent. cuprammonia or a mixture containing 0.192 per cent. $Ca(HSO_3)_2$ and 0.018 per cent. SO_2 proved fatal.

Again, parts of stems covered with pycnidia were plunged in various mixtures with a view of killing the spores in the pycnidia. When immersed in this way for 24 hours in a mixture of 0.288 per cent. $Ca(HSO_3)_2$ and 0.04 per cent. SO_2 the spores were killed. The same results were obtained with 10 per cent. sulfuric acid and with 10 per cent. sulfate of iron. When the stems were merely sprinkled with the same liquids the spores remained uninjured.

Further, spores developed in must containing 1 per cent. copper sulfate solution, only slightly in 2 per cent. solution, and not at all in a 3 per cent. A 0.3 per cent. solution of the calcium sulfite-sulfurous acid mixture proved fatal. These experiments were performed with a view of finding a method of combating the disease. The effect of such easily soluble and highly poisonous substances as the sulfurous acid mixture on living vines remains still to be determined.

It is remarkable that a work treating a serious fungous disease from an economic standpoint contains no record of field experiments for the control of the malady. The author's suggestions for combating the fungus are based mainly upon theoretical considerations and are for the most part impracticable, when not wholly at variance with long established principles of controlling fungous diseases.

[3] ISTVÁNFFI, GY. DE, Études sur le rot livide de la vigne (*Coniothyrium Diplodiella*). Ann. Inst. Ampélologique Royal Hongrois vol. 2. pp. vii + 288, *figs. 12*, *pls. 24*, double, colored. Budapest: Publications du Ministre Royal de l'Agriculture de Hongrie. 1902.

While the work is an excellent anatomical study of the fungus and its relation to the host, it contains little to elucidate the life-history of the fungus in nature, which, as the author remarks in the first chapter, is the only basis upon which defense is possible.—H. HASSELBRING.

MINOR NOTICES.

THE ACCOUNT of *Eucalyptus obliqua* L'Her., which is figured on four plates, forms part II of Maiden's *Critical revision of the genus Eucalyptus*. —C. R. B.

ENGELMANN has recently published the fifth fascicle of Dalla Torre and Harms's *Genera Siphonogamarum*,[4] including genera numbered 5183 to 6491.—C. R. B.

VOLUME 3 of the botanical series of the Field Columbian Museum is to be wholly devoted to *Plantae Yucatanae* by Dr. C. F. Millspaugh.[5] Dr. Millspaugh has been studying the plants of the insular, coastal, and plains regions of Yucatan for several years and has collected personally in this region. He has now begun the enumeration of the flora of the Antillean portion of Yucatan, which may be described as embracing roughly the portion of the state of Yucatan lying north of latitude 19° 30′. Fascicles will appear from time to time, as opportunity permits, without regard to the natural sequence of the orders, though they will be complete as far as the knowledge of the species permits. As a basis for the most important specific distinctions Dr. Millspaugh has selected the fruits and seeds, believing that these vary less than any others. Each species is illustrated by an inset figure, somewhat after the manner of Britton and Brown's *Illustrated flora*. These figures are admirably drawn by the author or by Miss Agnes Chase; unfortunately many of them have been sadly marred in the printing. If the copy which has reached us is a fair sample, we can only express surprise that the Museum should accept and issue such press work. It is extremely unfortunate that the excellent work of the author should be sent out in so unworthy a dress.—C. R. B.

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G. K. LEMMON describes in an out of the way place[6] a new lily, *Lilium Kelleyanum*, found near King's river, California, of which we make note that it may not escape attention.—C. R. B.

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LUTZ, after experimenting with certain fungi, suggests[8] that alkaloids in plants may be utilizable as plastic material when there is present an adequate supply of nitrates. So also a plant needs carbohydrates in excess before it can utilize asparagin. Lutz directs attention to the fact that certain plants (*e. g.*, aconite and belladonna) are rich in alkaloids when they grow in poor soil, but poor in alkaloids when cultivated in gardens, or when found in a soil rich in nitrates.—C. R. B.

MESSRS. SEWARD AND ARBER have critically examined a number of palm seeds from the Lower Tertiary of Belgium, England, France, and Italy.[9] The conclusion is reached, that they all belong to a single extinct species, *Nipadites Burtini* Brong. It is interesting, that at the present time a monotypic genus, *Nipa fruticans*, prevails in the Sunderbunds and in other southern Asiatic and Malayan deltas. The authors are of the opinion that the presence of *Nipadites Burtini*, together with other tropical forms of vegetation, in the early Tertiary beds of Europe make it extremely probable that a very much warmer climate prevailed at that epoch, than is now found in the same regions.—E. C. JEFFREY.

BENECKE, in an investigation of the formation of oxalic acid in green plants,[10] finds that maize plants form oxalates or not according as he supplies bases for combining with the oxalic acid. If nitrates be supplied, oxalate is produced; if ammonia salts (*e. g.*, sulfate) be used, no oxalate is formed. In other plants (Oplismenus, Fagopyrum, Tradescantia) he only succeeded in modifying the amount of oxalate by the culture conditions. The formation of raphides by Tradescantia was independent of external influences and could only be affected by the supply of calcium. In algae (Vaucheria, Spirogyra) no such relation could be determined. A useful summary of physiological literature of oxalic acid is given.—C. R. B.

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investigations show that about three-fourths of the ovules contain more than one embryo. A considerable percentage of the pollen is sterile and fertilization was not actually observed, although it probably occurs in many cases. Pollination is not necessary for the production of adventitious embryos, at least not for those coming from the nucellus. Whether an embryo would develop from an egg of Euphorbia without fertilization was not determined. Professor Hegelmaier withdraws his earlier statement that polyembryony, as found in Euphorbia, might lead to apogamy.— CHARLES J. CHAMBERLAIN.

IRREGULAR MITOSES in pollen mother-cells and the consequent formation of imperfect pollen have already been noted in several sterile hybrids. In *Cytisus Adami*[13] a hybrid between *Cytisus Laburnum* L. and *C. purpureus* Scop., the development of the pollen is regular, but abnormalities which result in sterility are found in the ovule. After the integuments are quite well developed, a region at the base of the nucellus, rich in protoplasm, begins to grow with great rapidity, so that the nucellus is soon forced out through the micropyle. Often no megaspore mother-cell can be detected; sometimes a larger cell with shrunken protoplasm and a few nuclei indicates that a mother-cell had begun to germinate, and occasionally when the nucellar growth is not particularly extensive, a normal embryo sac may appear. In both the parents the development of the embryo sac is regular.— CHARLES J. CHAMBERLAIN.

ZACHARIAS has published another paper[14] on the chemistry and structure of the nucleus. The present contribution deals with the contents of the nucleus, exclusive of the nucleus and nuclein-containing structures. Pollen mother-cells of Larix, Iris, Hemerocallis, and other forms were investigated. Material was examined in the living condition and also after treatment with various reagents, but sections do not seem to have been used. In dealing with nuclei in division after the nuclear membrane has broken down, the special term, nuclear cavity (*Kernraum*), is used, because the sphere of influence of the nucleus may not be the same as when the nuclear membrane is still intact. The writer believes that Němec's statement that the spindle fibers consist of plastin is too general. Plastin may be present in some cases, while in others it will be lacking. In the living cell during nuclear division the nuclear cavity, with the exception of the chromosomes, appears as if filled with a homogeneous fluid, in which movable thread-like structures may appear between the separating groups of chromosomes. Zacharias believes that his own investigations, as well as those of morphologists, show that definite spindle fibers have not yet been demonstrated in the living cell, and that it is possible that the structures seen in fixed material may be artifacts.—CHARLES J. CHAMBERLAIN.

[13] TISCHLER, G., Ueber eine merkwürdige Wachsthumserscheinung in den Samenanlagen von *Cytisus Adami* Poir. Ber. Deutsch. Bot. Gesell. **21**: 82–89. *pl. 5*. 1903.

[14] ZACHARIAS, E., Ueber die "achromatischen" Bestandtheile des zellkerns. Ber. Deutsch. Bot. Gesell. **20**: 298–320. *pl. 16*. 1902.

ASTRUC has brought to a conclusion his work on the acidity of plants.[15] He finds that in non-succulents vegetable acids are made chiefly in the young parts; that is, in the particular regions of cellular activity, of maximum turgescence, and of oxidation. These acids are neutralized or etherized little by little, as has already been shown by other observers. These facts serve to explain the distribution of relative acidity in plants, which gradually diminishes as the development of the organs advances. In succulents, on the contrary, the acidity depends upon slight changes in the external conditions, and these make comparisons sometimes difficult. Thus, the free acids in the Crassulaceae present within a single day enormous variation both in formation and in distribution, so that it is quite impossible to lay down any absolute rule for the occurrence of acids in different leaves of even the same plant. From a great number of experiments, however, Astruc has concluded that the formation of greater or less amounts of malic acid during the night depends on photosynthesis during the day, and is intimately related to respiration and to the greater or less value of the internal respiratory ratio during the night. Incidentally he notes a somewhat remarkable fact, that oxygen is not fixed by the cell when the protoplasm is anesthetized by ether or by chloroform. During the day malic acid diminishes in amount under the influence of respiration and photosynthesis, but if the normal conditions for the plant are changed, that is, if there intervene external causes capable of influencing cell activity, these causes will also influence acidity. Thus sectioning of leaves or changing the constituents of the atmosphere enveloping the plant will induce notable changes in the processes of acid formation or destruction. — C. R. B.

THE DEVELOPMENT of the sexual organs and fertilization in *Picea excelsa* are described in a recent article by Miyake.[16] The pollen grain at the time of shedding, about the second week in May, contains two disorganized prothallial cells, a stalk cell, body cell, and tube cell. The tube begins to form a few days after pollination, and the body cell at once passes into it and divides, giving rise to two male nuclei. At this division the beginning of a cell plate appears at the equator of the spindle, but it soon disappears and no wall is formed; consequently the two male nuclei lie free in a common mass of cytoplasm, and there is no formation of two cells, as described by Strasburger, Belajeff, Dixon, and Coulter. The pollen tube does not branch.

The development of the archegonium is very much as in Pinus. In the neck of the archegonium there are 4–8 cells with 2–4 cells in a row. There are usually four archegonia to each ovule, but the number varies from two to seven. During the growth of the egg no passage of nuclear material from

[15] ASTRUC, M. A., Recherches sur l'acidité végétale. Ann. Sci. Nat. Bot. VIII, **17**: 109. 1903.

[16] MIYAKE, K., On the development of the sexual organs and fertilization in *Picea excelsa*. Ann. Bot. **17**: 351–372. *pls. 16–17*. 1903.

the jacket cells into the egg could be detected. The ventral canal cell is formed about a week before fertilization, which, in the neighborhood of Ithaca, occurs about the middle of June. No walls are formed in the proembryo until it has reached the eight-celled stage. Strasburger described walls at the four-celled stage, and other writers have described walls at the four-celled stage in Pinus.

The antheridial cell of Strasburger (third prothallial cell of Belajeff) is called the central cell by Miyake, who regards it as the equivalent of the central cell in the antheridium of pteridophytes. The body cell of Strasburger is called the generative cell. Strasburger refers to the two male cells as generative cells. The terminology is confusing and we are not sure that the present writer has been entirely consistent.—CHARLES J. CHAMBERLAIN.

PLANT HYBRIDS have received but little attention from cytologists. It is known that various species of a genus usually have the same number of chromosomes and that the pollen of sterile hybrids usually have imperfect pollen. Rosenberg[17] has been fortunate in finding a hybrid between parents which differ from each other both in the number and size of their chromosomes. This hybrid is *Drosera rotundifolia* × *longifolia*. *D. rotundifolia* has twenty chromosomes in the sporophyte, this number appearing in the stem, leaf, and root. The chromosomes are short and easy to count. In the pollen mother-cell the number is always ten. In *D. longifolia* the vegetative tissues show forty chromosomes and the pollen mother-cells twenty, just double the numbers in the other species. The chromosomes are also distinguished by being somewhat smaller than in *D. rotundifolia*.

The hybrid is easily recognized by external characters, but is also distinguished by its chromosomes. The mitoses are not different from those of the parents except in the number of chromosomes and the consequent variation in the shape of the spindle. In the sporophyte thirty chromosomes, the sum of the gametophyte numbers of the two parents, was counted in the root, stem, and leaf. In a few cases forty chromosomes appeared in the tapetal cells. In the pollen mother-cells fifteen chromosomes is the dominant number, but twenty often occur, and occasionally mother-cells with ten are found. All three numbers have been found in the same anther. The megaspore mother-cell was not investigated.

The relative number of chromosomes in the parents and hybrid support the theory that the chromosome is a permanent organ of the cell. The fact that three kinds of pollen grains are formed has its bearing upon Mendelism. Professor Rosenberg will continue these investigations.—CHARLES J. CHAMBERLAIN.

IN THE FIRST of a series of studies on the anatomy of ferns, entitled "La masse libéroligneuse élémentaire des Filicinées actuelles et ses princi-

[17] ROSENBERG, O., Das Verhalten der Chromosomen in einer hybriden Pflanze. Ber. Deutsch. Bot. Gesell. **21**: 110–119. *pl.* 7. 1903.

paux modes d'agencement dans la fronde," Bertrand and Cornaille[18] describe and discuss, from the taxonomic and anatomical standpoint, the constitution and arrangement of the fibrovascular strands in the leaves of various living orders of ferns. They point out that the petiolar bundle-system of ferns is composed of various combinations of units which they denominate "divergents." Each divergent consists of a protoxylem group placed anteriorly, *i. e.*, toward the upper surface of the frond, and two wings of metaxylem growing out of this posteriorly, *i. e.*, toward the lower surface of the frond. The wood so constituted is typically covered, both dorsally and ventrally, by layers of phloem. The petiolar bundle-systems of the various groups of living ferns may either be gamodivergent, consisting of a number of divergents more or less completely fused together, or dialydivergent, where the divergents are more or less completely separated from each other. In addition the bundle-system as a whole may present various degrees of complexity in the curvatures presented by a line drawn so as to connect all the bundles in a given petiole, etc. The authors point out that there are two striking differences between the petiolar fibrovascular system of the ferns (or Megaphyllides as they term them) and that of the cycads; for in the latter the fibrovascular units corresponding to the divergents, instead of having two wings as in the ferns, are monopolar, and further the protoxylem, instead of being placed anteriorly and toward the upper surface of the leaf is posterior and next the lower surface of the frond, being thus centripetal as in the lycopods. The authors are of the opinion that there should, as a consequence of these differences, be a good deal of reserve in the matter of deriving the cycads from a filicineous stock, as is the almost universal tendency at the present time.— E. C. JEFFREY.

THE formation of the spores in *Rhizopus nigricans* and *Phycomyces nitens* is described by Swingle in a recent *Bulletin*[19] of the Bureau of Plant Industry. Pure cultures were obtained, the material was fixed, sectioned, and stained, according to the most approved cytological methods. The paper deals especially with the mechanics of the peculiar cell division found in these sporangia, and with the nature and functions of the vacuole. It is of interest to note that the four genera of the Mucorineae which have now been carefully investigated, Pilobolus and Sporodinia studied by Harper, and Rhizopus and Phycomyces studied by the present writer, differ considerably in the formation of their spores. The following is Swingle's own summary of the process:

[18] BERTRAND, C. E., and CORNAILLE, F., Étude de quelques caractéristiques de la structure des Filicinées actuelles. Travaux et Mémoires de l'Université de Lille **10**: —. 1902.

[19] SWINGLE, DEANE B., The formation of spores in the sporangia of *Rhizopus nigricans* and *Phycomyces nitens*. U. S. Dept. of Agric., Bureau of Plant Industry, Bull. 57. pp. 40, *pls.* 6. 1903.

1. Streaming of the cytoplasm, nuclei, and vacuoles up the sporangiophore and out toward the periphery, forming a dense layer next the sporangium wall and a less dense region in the interior, both containing nuclei.

2. Formation of a layer of comparatively large, round vacuoles in the denser plasm, parallel to its inner surface.

3. Extension of these vacuoles by flattening, so that they fuse to form a curved cleft in the denser plasm; and, in the case of Rhizopus, the cutting upward of a circular surface furrow from the base of the sporangium to meet the cleft formed by these vacuoles, thus cleaving out the columella.

4. Division of the spore-plasm into spores; in Rhizopus, by furrows pushing progressively inward from the surface and outward from the columella cleft, both systems branching, curving, and intersecting to form multinucleated bits of protoplasm, surrounded only by plasma-membranes and separated by spaces filled with cell sap only; in Phycomyces, by angles forming in certain vacuoles containing a stainable substance and continuing outward into the spore-plasm as furrows, aided by other furrows from the columella cleft and dividing the protoplasm into bits homologous with and similar to those in Rhizopus, and separated by furrows partly filled with the contents of the vacuoles that assist in the cleavage.

5. Formation of walls about the spores and columella, and, in the case of Rhizopus, the secretion of an intersporal slime.

6. Partial disintregration of the nuclei in the columella.—CHARLES J. CHAMBERLAIN.

AN EXCELLENT ACCOUNT of the sexual processes in *Plasmopara alpina* Johans. by Rosenberg[20] adds another form to the list of Phycomycetes which are now receiving so much attention.

Plasmopara conforms in all essentials to the condition in Peronospora and Albugo. The oogonium contains at first about forty-five nuclei, which number is doubled by the first mitosis. All of these pass into the periplasm excepting one, which remains in the ooplasm near a coenocentrum. There is then a second mitosis, affecting almost all of the nuclei. The nucleus in the ooplasm divides, forming the female nucleus, which remains close to the coenocentrum, and a sister nucleus that passes to one side and breaks down. Thus proximity to the favorable conditions around the coenocentrum determines the selection of the functional gamete nucleus here as in others of the Peronosporales and in the Saprolegniales.

The antheridium contains at first about five nuclei, which are increased to ten or twelve by mitosis. One male nucleus is introduced into the egg and fuses with the female.

Of especial interest are Rosenberg's views on the significance of the mitosis in the oogonium and antheridium. The author considers these as

[20] ROSENBERG, O., Ueber die Befruchtung von *Plasmopara alpina*. Bih. Svensk. Vet.-Akad. Handl. **28**:—. [1–20. *pls.* 2.] 1903.

comparable to the tetrad divisions in higher plants, meaning the two mitoses in the spore mother-cell. The nucleus passes through a synapsis condition before the first mitosis. The spindle is intranuclear with small granular bodies at the poles as in others of the Peronosporales. In the second mitosis the spindle is less distinct, as Stevens noted in Albugo. The number of chromosomes appears to be about the same in each mitosis. Rosenberg regards the synapsis as indicating a reduction of the chromosomes, in agreement with the generally accepted history of the spore mother-cell, and considers its presence in relation to the two mitoses as establishing analogies with these events.

The reviewer has recently discussed the behavior of the nucleus during gametogenesis in the Phycomycetes[21] and regrets that he could not have included Rosenberg's views in that account. However, his opinions are not changed by these results. It is not established that synapsis has any relation to reduction phenomena in the thallophytes, and it is also being reported among higher plants in tissues where there is no reduction. The number of mitoses in the gametangia of Phycomycetes is quite variable. There is only one in the oogonium of Saprolegnia and in certain species of Peronospora and Pythium. This mitosis is probably a phylogenetic reminiscence of times when many gametes were formed in these gametangia. A second mitosis is probably merely a continuation of the tendency to multiply the nuclei and would be carried farther if nutritive conditions allowed. The second mitosis is more likely to be found in the ooplasm, because that portion of the cell is unquestionably better nourished, which explains its entire or partial absence in the periplasm. There is excellent evidence that the second mitosis is weaker in kinoplasmic material than the first, thus showing the effect of unfavorable conditions in the cell.

This is not saying that reduction phenomena may not take place just previous to the mitoses in the gametangia of Phycomycetes, but comparisons between these mitoses and the events in the spore mother-cell are not likely to have much value in establishing the supposition. To the reviewer the probabilities seem all against the existence of reduction phenomena previous to gametogenesis in plants, for it is more natural to expect it either immediately after the sexual act or at the end of a sporophyte generation. The proof must come through studies of the nucleus at various periods of ontogeny and the evidence will accumulate slowly. We do not know of any better forms for such investigations than some of the Peronosporales, unless they be certain Chlorophyceae which have not received their fair share of attention in the cell studies of recent years.— B. M. Davis.

Rothert has studied the effects of ether and chloroform on the sensibility of microorganisms.[22] Knowing that narcotics affect the various functions of

[21] Davis, B. M., Oogenesis in Saprolegnia. Bot. Gaz. **35**: 339–342. 1903.

[22] Rothert, W., Ueber die Wirkung des Aethers und Chloroforms auf die Reizbewegungen der Mikroorganismen. Jahrb. Wiss. Bot. **39**: 1–70. 1903. The title is

higher animals differently according to the concentration and duration of action, so that the effects can be arranged in a graded series, he proposed to himself the solution of the question whether a similar gradation in narcosis existed among plants and the protozoa, in which the differentiation and division of labor has not gone so far. If, for example, their sensitiveness to external stimuli could be suspended more easily than other vital phenomena, it would be possible by partial narcosis to make them insensitive (*i. e.*, to produce anesthesia), without at the same time suppressing those functions (growth, movement, etc.) by means of which a visible reaction could be executed. Thus an important means of analyzing irritable reactions might be secured.

After securing suitable material (a matter of great difficulty), tests were made (1) by putting organisms into vials containing water with known percentages of the narcotic, with precautions against its evaporation; (2) by using mounted preparations, the cover being supported, in which were introduced Pfeffer's capillary tubes (for chemotaxis) or air bubbles (for aerotaxis); or (3) by means of hanging drop cultures in a moist chamber. The criterion for the existence of sensibility was the accumulation of the individuals in definite regions.

Naturally, though not the chief aim, many observations were made on the effect of narcotics on motility. The resistance of nearly related organisms is very different; *e. g.*, one form of *Bacterium termo* ceased to move in 20 per cent. ether-water,[23] while many individuals of another form, apparently the same species, resisted a saturated solution of ether for five hours. Similarly *Gonium pectorale* has its movements slowed by 2.5 per cent. ether-water and wholly stopped by 20 per cent.; whereas *Chlamydomonas sp.?* moved normally in 20 per cent. ether-water and was only stopped by 60 per cent. Individual differences are also noticeable.

Rothert found various forms in which the osmotactic, chemotactic, aerotactic, or phototactic sensitiveness could be suspended by the narcotics, while movement was not. Thus in one form of *B. termo*, chemotaxis and aerotaxis were only slightly reduced by moderate concentrations, while osmotaxis was completely checked. In *Bacillus Solmsii* chemotactic sensibility was stopped by chloroform but not by ether.

A curious reversal of phototactic reaction occurred with chloroform, both in Chlamydomonas, which cannot be anesthetized, and in Gonium, which is easily made insensible. These organisms, which were reacting negatively,

inappropriate to the paper, for Rothert specifically says (p. 15): "The question as to the influence of narcotics upon the motility of microorganisms I did not consider the object of my investigations." Nor are the researches confined to "microorganisms," as this term is commonly used, though all the forms studied were microscopic.

[23] *I. e.*, a 20 per cent. solution of a saturated solution of ether in water at room temperature; similarly designated in other cases.

immediately upon treatment with weak chloroform-water reacted positively. In other words, the critical intensity of light (*i. e.*, the point at which a given organism will not react) was raised by the chloroform, so that what they fled from before, they now sought. This effect disappears gradually, and the faster the weaker the chloroform. Ether produces no such effect. Immediately after a phototactic organism recovers from a dose of ether or chloroform, its reaction is always negative. If normally positive, the reaction is reversed; if normally negative, the reaction is intensified; *i. e.*, the critical intensity of light is lowered.

The results reached by Rothert regarding the specifically different susceptibility of related forms to narcosis are quite irreconcilable with the statements of Overton, who holds[24] that this susceptibility depends on the grade of differentiation of the cells, as indicated by the rank of the organism. Even individual differences were found by Rothert to be great.

It is found to be characteristic of the anesthetic effect of ether and chloroform on microorganisms that it depends only upon their concentration and not upon the duration of their action. Anesthesia appears instantly and disappears as quickly. No solution which is too weak to effect anesthesia at once will produce it by prolonged action. Some observations indicate that solutions too weak to produce complete anesthesia will diminish the degree of sensitiveness to stimuli. The effect of these narcotics on movement, however, is quite different; for this depends both on their concentration and the duration of their action.

This paper adds valuable data to our present knowledge of the narcosis in plants, for which previously we have been chiefly indebted to Overton.—C. R. B.

[24] Studien über die Narkose. Jena. 1901.

OPEN LETTERS.

Flora of St. Croix.

I HAVE, quite by chance, just come across *The flora of the island of St. Croix*, published by C. F. Millspaugh in the Feld Columbian Museum Bot. Series, Vol. I, no. 7, which was issued at the end of last year. In Mr. Millspaugh's work no notice whatever is taken of the species published by Mr. Paulsen and the writer in a floristic appendix to our work "Om Vegetationen paa de dansk-vestindiske Öer;" though Mr. Millspaugh in his introduction gives a complete translation of the lines from Urban's "Bibliographia" dealing with our work: "In a floristic appendix six phanerogams new to the Danish islands and Rostrup's fungi and lichens are listed."

We are thus led to believe that the author has not taken the trouble to read our paper.[1] Nor has he apparently made himself acquainted with the additions to Urban's "Bibliographia," which occur in later numbers of the *Symbolae Antillanae*. The result is that none of the species of phanerogams, fungi, and lichens published by us have been included. The author also gives a short list of algae, containing, according to his typography, species new to the island. But hardly any of them are really new, as almost all of them, and several others, are mentioned in my short paper, "A contribution to the knowledge of the marine algal vegetation of the coasts of the Danish West-Indian islands." I have, moreover, distributed some St. Croix algae in Wittrock and Nordstedt's exsiccatae, and in Phycotheca Amer.-bor.

It is of course of great interest to have the new finds in St. Croix published, but this could have been done as an appendix to the flora of the islands. But when Mr. Millspaugh sets out to give a complete list, we are justified in expecting that everything published regarding the flora of the islands will be included.—F. BÖRGESEN.

IT IS distinctly stated on page 459 of the publication referred to that it *only* includes the work of the Rickseckers, checked by the only published general list of the island flora, viz., Eggers's. It was not the intention to include scattered lists. All of Urban's publications which were available up to the date of sending in copy were made use of.—C. F. MILLSPAUGH.

[1] Bot. Tidskrift, 1898, and Revue Gén. Bot., 1900.

NEWS.

DR. B. E. LIVINGSTON has been granted a research scholarship by the New York Botanical Garden, where he will spend some months on leave of absence from the University of Chicago.

HOMER R. FOSTER, for the past five years professor of botany in the University of Washington, has resigned to take up commercial work in connection with a large hardwood lumber firm in Chicago.

CHARLES J. BRAND, who for the past year has been assistant in plant economics at the Field Columbian Museum of Chicago, has been promoted to the position of assistant curator, department of botany, in that institution. Mr. Brand is a graduate of the University of Minnesota.

MR. C. G. LLOYD, of Cincinnati, seems to have been elected a member both of the German Botanical Society and of the Botanical Society of France. Though the Germans print the name L. G. and the French C. J., it is doubtless our well-known mycologist who is intended in both instances.

THE FRENCH NATIONAL SOCIETY of Agriculture has awarded a gold medal to M. Lucien Daniel for his researches on grafting; a silver medal to M. Paul Parmentier for his *Traité de botanique agricole;* and a bronze medal to M. Th. Husnot (best known as a bryologist) for a book on *Les pres et les herbages.*

THE BOTANICAL GARDEN of Buitenzorg has begun issuing still another publication, entitled *Icones Bogonienses*, in which are to be described and figured new or little-known species of the Dutch possessions, or species cultivated in the garden. Four fascicles have already appeared, and others are to be published at irregular intervals.

THE HERBARIUM of the late Alexis Jordan has been acquired by the Catholic University of Lyons. The duplicates are to be sold, at prices varying from 20 fr. to 12 fr. per 100, according to the completeness and quality of the sets. The best will contain from 7,000 to 12,000 species. Applications may be made to Professor Roux, rue du Plat, Lyons, France.

EDMUND P. SHELDON and M. W. Gorman have undertaken a botanical expedition to the "Three Sisters," snow peaks of the Cascade range in Oregon. These mountains, unnamed and for the most part unknown, are all over 10,000 feet high, and the obsidian cliffs, glaciers, and waterfalls of the region are said to be wonderful. It is likely that the trip will yield a large number of interesting plants.

THE VERMONT BOTANICAL CLUB held its ninth annual field meeting at Arlington and Manchester in southern Vermont on July 3 and 4. There was a good attendance, including visiting botanists from Minnesota, New York, Massachusetts, and New Hampshire. The weather was ideal and the ascent of Mt. Equinox, under the guidance of Judge and Mrs. Loveland Munson, was a delightful mountain climb which afforded much of botanical interest. This club now has about one hundred and sixty active members.

DR. H. G. TIMBERLAKE, assistant professor of botany in the University of Wisconsin, died suddenly on July 19 at the age of thirty. He was taking a bath and seems to have slipped on the curved bottom of the enameled tub and fallen over the side, striking his head violently on the floor and rupturing a cerebral artery. Death occurred before a physician could reach him. Dr. Timberlake had recently been promoted to an assistant professorship and was married on June 30 to Miss Violet Slack, an assistant in the department.

THE COMMITTEE OF ORGANIZATION for the International Botanical Congress at Vienna plans to have the meetings on June 13–18, 1905, giving the mornings to addresses and discussions of topics of present importance (a morning to some one subject), and the afternoons to the nomenclature problem. The morning of the fifteenth will be reserved for a meeting of the Association internationale des botanistes. A great botanical exposition is planned, at the time of the Congress, in the palace at Schönbrunn; and excursions, botanic and scenic, before and after the Congress, will be arranged.

IT IS PROPOSED to organize a society for horticultural science, the object of which shall be more fully to establish horticulture on a scientific basis. The membership will naturally be made up of the horticulturists of the experiment stations and of the U. S. Department of Agriculture, together with other scientific men whose work has a horticultural bearing. The meetings will be held in connection with those of some kindred society, as the American Pomological Society or the American Association for the Advancement of Science. Any botanists interested are requested to address S. A. Beach, Horticulturist, New York Agricultural Experiment Station.

WITH THE TENTH VOLUME the *Annuario del Real Istituto Botanico di Roma*, founded by Professor R. Pirotta in 1884, comes to an end. In its place there is to appear the *Annali di Botanica*, which will be published in small fascicles in order to avoid the long delay of a more voluminous journal. The new publication will include not only original researches in all fields of botany, but also analytical reviews of important papers and synthetical reviews of current questions. Particular attention will be given to the history of botany in Italy and to making known all facts regarding the Italian flora. The first fascicle was published on May 15, and the second on June 30.

VOLUME XXXVI NUMBER 3

BOTANICAL GAZETTE

SEPTEMBER, 1903

THE VEGETATION OF THE BAY OF FUNDY SALT AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.[1]

W. F. GANONG.

(WITH SIXTEEN FIGURES AND MAPS)

AT the head of the Bay of Fundy, in the Provinces of New Brunswick and Nova Scotia, occur extensive and diversified salt marshes. In places they merge into fresh-water bogs; elsewhere, and for most of their area, they are reclaimed from the sea and in a high state of cultivation, or are in process of reclamation; and some parts remain still in their natural state. Corresponding with these marked differences of conditions are striking differences in the vegetation; and the constant operations of diking, flooding, etc., allow all gradations of conditions, and hence of vegetation, to be seen. There is here offered, therefore, an unusually favorable opportunity to investigate some phases of the dynamical relations of plants to their environment, particularly the effects of soil and water upon their forms and sizes, upon the determination of the kinds that occur in such places, and upon the succession of one kind by another. In the present paper are contained the results of the observations I have

[1] No. 1. Upon raised peat-bogs in the Province of New Brunswick. Trans. Roy. Soc. Canada II. 3[1]: 131–163. 1897.

No. 2. A preliminary synopsis of the grouping of the vegetation (phytogeography) of the Province of New Brunswick. Bull. Nat. Hist. Soc. New Bruns. 5:47–60. 1903.

The present paper was presented in abstract before the Society for Plant Morphology and Physiology at the Yale meeting, December 28, 1899.

been able to make upon these subjects during some eight weeks of field work in the summers of 1898, 1899, and 1901, together with such a summary of the origin and development of the marshes as seems necessary to an understanding of the present subject.

Literature and other sources of information.

From the present, or indeed, from any, point of view, there is practically no scientific literature upon the vegetation of these marshes. A very brief list, of but six species, of the plants characteristic of the wild salt marsh was given by Goodwin in 1893, and references to a species or two occur in some of the papers later to be cited; but further there is nothing. Upon the geological origin, structure and economics of the marshes, however, there are valuable publications to be mentioned later. As to the literature of salt marshes in other parts of America, this also is scanty. Shaler, in two or three of his works, has given brief descriptions of the mode of formation and economics of those of the Atlantic coast of the United States, and, recently, valuable contributions have appeared by Kearney, by Harshberger, and by Lloyd and Tracy. There are references to salt marshes in Warming's and in Schimper's well-known general works, and there are papers on the salt marshes of Europe by Warming, by Flahault and Combres, and by others, and there is a synopsis of those of Germany in Drude's work.

Any account of the changes in vegetation brought about in the process of reclamation of the sea-bottoms in the Netherlands would be of interest in this connection, but such I have not found, nor have I been able to see a paper by Theen on the diked marshes of Schleswig-Holstein, mentioned by Drude (p. 390). Upon bogs, into which the marshes often merge, there is of course an ample literature, partly summarized in the first paper of this series. All of the works above-mentioned will be referred to their proper places later, and are cited in full in the bibliography at the end of this paper.[2]

[2] In the marsh country there are residents who are experts in all matters pertaining to the economics of the marshes, and from several of them I have obtained most valuable information, which I wish here gratefully to acknowledge. I am particularly indebted in this way to Mr. W. C. Milner, of Sackville, President of the Misse-

The distribution and extent of the marshes.

The marshes now under discussion possess, as will later be shown, peculiarities which clearly differentiate them from the ordinary salt marshes so common everywhere about the mouths of tidal rivers in this country and in Europe, and hence are of a type rare if not unique. The ordinary marshes are also abundant in this region (though of small extent), particularly along the Gulf of St. Lawrence shore. Others, more like those we are considering, occur in the Bay of Fundy at Annapolis Basin, at Musquash, at Pisarinco, at St. John, at St. Martins, at Martins Head and elsewhere, sometimes diked and sometimes not. But in their complete and perfect form, the Fundy salt marshes are confined to the two heads of the Bay, *i. e.*, to Minas Basin and Chignecto Bay; and they are largest and finest in the latter. Their extent and distribution are very clearly shown upon the surface geology maps of this region, and, for Chignecto Bay, in the accompanying map (*fig. 1*). In Chignecto Bay they begin at Rougie (or Petit Rocher), just west of Cape Enrage, and thence extend irrregularly to the Shepody River; they occur in places along the Petitcodiac and Memramcook Rivers, and reach their perfection of size, economic value and scientific interest at the head of Cumberland Basin, whence they radiate up the valleys of the several small rivers of that district, the Tantramar, Aulac, Misseguash, LaPlanche, and (to a lesser extent) the Nappan, Maccan and Hebert. Largest of all is the combined Tantramar-Aulac marsh, shown in detail upon the accompanying map (*fig. 2*), and it is this, with the Misseguash marsh and the Shepody marsh, that I have studied.

The total area of the marshes with the related bogs is only approximately known. In 1895, Mr. Chalmers, of the Geological Survey, after a careful computation, estimated 34,300 acres of diked and undiked marsh in New Brunswick, of which 9,100 acres were in Albert county west of the Petitcodiac, and 25,200 in Westmorland north of the Misseguash. Mr. Monro, a profes-

guash Marsh Co.; to Mr. Howard Trueman, of Point de Bute; and to Mr. William Fawcett, of Upper Sackville. Mr. F. A. Dixon, of Sackville, has aided greatly by collecting for me seeds of many of the marsh plants.

sional surveyor who was engaged upon all of the principal surveys of these marshes, estimated in 1883 that the diked marsh (the undiked is comparatively insignificant in quantity) on the Nova Scotia side of the boundary contained 12,600 acres, while New Brunswick had on the Tantramar, Aulac and Misseguash,

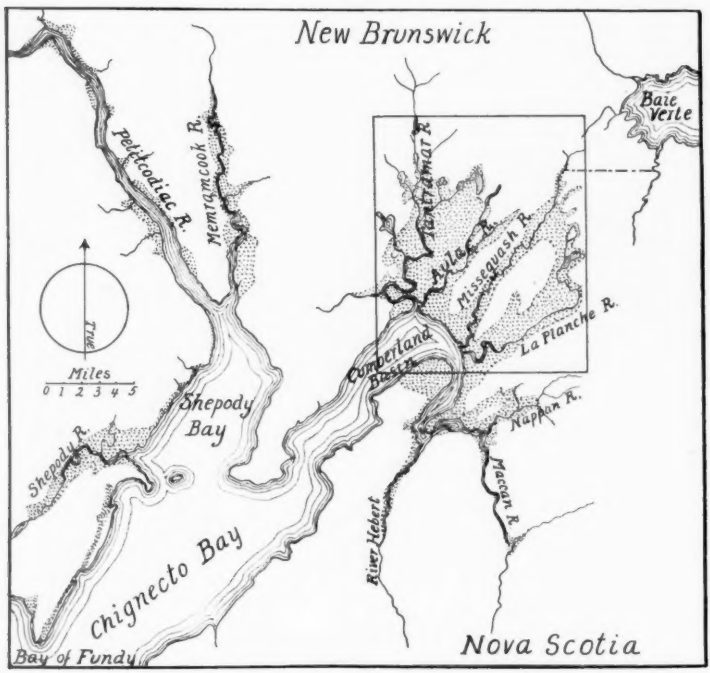

FIG. 1.—Sketch map of the marsh country, showing (dotted) the distribution of the principal marshes. The area enclosed by the quadrangle is shown enlarged in *fig. 2*.

19,400 acres. Of still unreclaimed bog lands (everywhere underlaid by marsh), there were on the LaPlanche 1,000 acres, on the Misseguash 3,700 acres, and on the Aulac and Tantramar 4,000 acres. Thus there are about 40,700 acres of marsh and bog about Cumberland Basin, of which 25,000 acres belong to New Brunswick, and 15,700 acres to Nova Scotia. Their approximate extent in this vicinity, and the relative amounts of wild

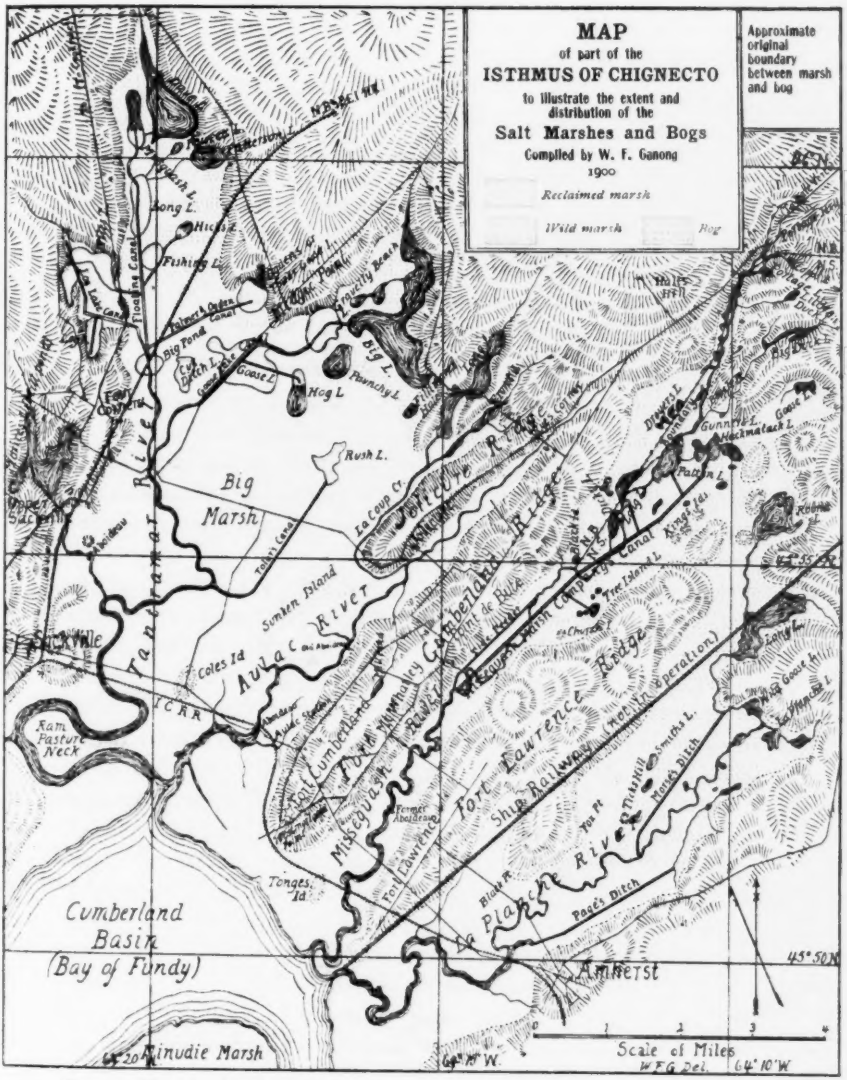

FIG. 2. — Map showing the distribution of the principal salt and diked marshes and bogs.

and reclaimed marsh and bog, together with the outlines of these marshes, may be gathered from the accompanying map (*fig. 2*) drawn to the scale of two miles to an inch. The marshes on Minas Basin are much less in area than those on Cumberland Basin, but in the aggregate there are at the head of the Bay of Fundy not far from 70,000 (or as Hamilton estimates, 80,000) acres of marshes and bogs, of which by far the greater part is diked and under cultivation. The extent of the diked marshes may be yet better understood when it is stated that, according to Shaler, the entire area of all of the diked salt marshes of the eastern United States does not exceed 5,000 acres.

The characteristics of the marsh country.

The country around Cumberland Basin is of ancient (Palaeozoic) formations, rounded into low smooth hills and ridges separated by radiating river valleys. Among the ridges lie the marshes, seemingly level as the sea; and, like it, they fill bays, surround islands and are pierced by points. Seen from the neighboring ridges, the marshes have an aspect characteristic and beautiful. They are treeless, but are clothed nearly everywhere with dense rich grasses in many shades of green and brown, varying with the season, with the light, and even with the winds. For the most part the merging of the colors is irregular; but in places, owing to the different treatment given by different owners to their land, or to the presence of fields of grain or pasture-lots, there is something of the checkered appearance usual in highly cultivated land. The frequent ditches marked by denser growths, the rare fences and the occasional roads or railways are other signs of the operations of man. Towards the sea are narrow fringes of unreclaimed marsh, poorer in vegetation and generally duller in color, while farther back the green of the marshes gives place to the brown and gray of the bogs, which are further distinguished by irregular shrubbery and trees, and many little lakes. Nobody lives upon the marshes, but scattered upon them are many great barns, all of one and the simplest pattern, unpainted and gray from the weather, standing at any and every angle. These barns are one of the distinguishing features of the marshes, and give to

them a suggestion of plenty which is a true index of the economic condition of this region, for here are the most prosperous and progressive farmers, and the most thriving country towns in eastern Canada. Especially characteristic of the marshes are the tidal rivers which have helped to build them. As is well known, the sea here shows a great range of tides, even to over forty feet.[3] The tidal rivers, winding in the most sinuous courses through the marshes, at times run full to their bordering dikes, loaded with brownish-red mud; but the fall of the great tides sends their thick currents tumultuously out, to leave but tiny rills between deep gaping gashes of slippery mud gleaming in the sunlight. Thus too are extensive flats laid bare about Cumberland Basin. The suspended mud gives both to the rivers and to the sea a dull-red color which is a striking and a characteristic feature of the scenery of the marsh country. Not all of the rivers, however, are red, for from some of them the sea has been shut out by ingenious dams, and in each of these the banks are clad with dense green grass to near the bottom of the bed, along which winds a small fresh-water stream.

When one goes upon the marshes from the upland, he is likely to think them misnamed; for instead of the soft bottom and the rank growth associated with the word marsh, he finds everywhere a soil as firm as the upland itself, and, on the reclaimed parts, a growth of the finest grasses, luxuriant but not coarse. Indeed, a near view of the reclaimed marsh shows scarcely anything different from the best of fine-soiled upland grass land.

The marsh country is beautiful to look upon, and in addition there hovers over it the charm of a long and varied history. It was a part of the ancient Acadia and inherits the memories of

[3] The height of the tides in this region is popularly exaggerated. Careful measurements have given for Cumberland Basin a range of 38 feet for neap and of 45.5 feet for spring tides. Exceptional tides have had greater range, and the greatest on record (the Saxby tide of 1869) had a range of about 70 feet. The tides at the head of Minas Basin are ordinarily somewhat higher than in Cumberland Basin. Fuller particulars may be found in the Admiralty charts, in a "Report . . . . on the construction of a canal between the Gulf of St. Lawrence and the Bay of Fundy," Ottawa, 1874, and in a Report on a "Survey of tides and currents in Canadian waters," by W. Bell Dawson, Ottawa, 1899.

that picturesque but ill-fated country. The student in his wanderings meets with many a reminder of the ancient régime.

The geological origin of the marshes.

An understanding of the origin and formation of the marshes is so important to the interpretation of some of the peculiarities of their vegetation, that a somewhat full account of it is needful here.

The subject was first touched upon by Lyell (in his *Travels in North America*, 1845), but received its first systematic discussion from Dawson (in his *Acadian Geology*, 1855, repeated in later editions). Subsequent accounts, with some additional facts, are given by Monro (1883), by Chalmers (1895), by Trueman (1899), and in more popular fashion by Dixon (1899); while an extremely good synopsis of the whole subject has been contributed by Eaton (1893). From the point of view of the tidal action in their formation there are papers by Hamilton (1867), by Matthew (1880), and by Murphy (1886), and of course scattered references by others.

The central fact in the formation of the marshes is this: they have been, and still are being, built in a subsiding basin out of inorganic red mud brought in from the sea by the rush of the tides, whose height is the determining factor in their height. Practically no part of their mass has been built from detritus brought down by rivers, which in this region are altogether insignificant in volume; nor has vegetation, either marine or land, helped to any appreciable extent to build them. I believe no observer of the mode of their formation could doubt that they would be as high and wide as they are today had never a plant grown about or upon them. It is these two facts, their formation out of a purely inorganic mud brought in by the sea, and the lack of cooperation of plants in their building, which differentiate them from the salt marshes so common elsewhere about the mouths of tidal rivers.

Whence, then, comes this great store of rich mud? On this all students agree; it is from the red Permo-Carboniferous sandstones forming the sides and bottoms of the channels between the marshes and the Bay of Fundy. These soft rocks are

rapidly eroded by the strong tidal currents, which, in their onward rush to the northeast, carry the detritus whirling in suspension, to drop it as their force is checked by their quiet spread over the marshes at the highest tides. Thus, the sea bottom supplies the materials, the rush of the tidal currents the power to remove, carry and lift them, and the quiet of the waters at the turn of the tide the condition allowing them to be dropped. In this way the sea is building up the land, perhaps on a greater scale here than elsewhere on the globe.[4]

The quantity of mud needed to form the marshes has been immensely great. Not only do they cover many square miles, but borings show that they can be as deep as eighty feet at least ;[5] and moreover, the marsh mud extends also everywhere under the bogs and shallow lakes clear to their utmost bounds. To supply this quantity, the channel to the bay (Chignecto Channel) must have been enormously widened and deepened, and hence it must have been very small when the process began. The sea has quarried out the channels, and the marshes are the debris. This process has been aided, or, perhaps more properly, has been allowed, by the recent subsidence of this region, of which the indisputable evidence is found in the buried forests well known to exist at several points under the marsh much below high-tide level. Dawson first described the stumps of a beech and pine forest, the wood still sound, rooted on Fort Lawrence Ridge, thirty to thirty-five feet below high-tide level. Chalmers and others have described other cases, particularly stumps laid bare, over thirty feet under the surface, in the ship-railway dock,[6] and I

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[5] Chalmers, Geological Report 1885, M, 129 : according to the same investigator however (*op. cit.* 41) this depth appears to be so great in consequence of a fault at this place. He apparently means that the downthrow took place while the mud was accumulating. The depth of 150 feet assigned to the mud at this place by Trueman, is based, as he informs me, upon the recollection of a resident as to the depth of the boring described by Mr. Chalmers. The official figures of the latter, however, make the depth somewhat under 80 feet.

[6] The ship-railway, a great work designed to transport vessels across the Isthmus of Chignecto by rail in lieu of a canal. Though over three-fourths finished, work upon it has been suspended and is unlikely to be resumed.

have myself seen such stumps in position. The soundness of the wood shows how recent the subsidence must have been. Another fact important in this connection is the presence of a bed of peat twenty feet thick under eighty feet of marsh mud, as shown by a boring at Aulac described by Mr. Chalmers. The same observer has also found that in other places the marsh mud is underlaid by post-glacial clay containing shells of species still living in this region, though in clearer and quieter waters than now prevail in Cumberland Basin, and that this clay merges without break into the marsh mud. Grouping together these facts, the history of the marshes would appear to have been as follows. At a comparatively late post-glacial period, the land must have stood much above its present level.[7] At that time the present Cumberland Basin was a shallow lake around which peat bogs were growing; it received the waters of the seven small rivers still flowing into it, and emptied by a single narrow fresh-water channel along the course of the present Cumberland and Chignecto Channels.[8] The subsidence of the land (the same which has drowned the lower valleys of the St. John, St. Croix and other rivers of this region), allowed the tide to creep farther and farther up this channel until it reached the lake above, which it converted into a brackish, and later a salt, lagoon. At first the water would not be very muddy nor the tidal fluctuations great in the lagoon; but as the land continued to sink, the currents would become more powerful, erosion more active, and the water so muddy that marsh formation would begin around the margin of the basin and at the head of tide on the rivers. Thus, gradually, the conditions of the present day were brought about.[9]

[7] Not necessarily over 80 feet, the greatest known depth of the marsh mud, and even much less if Chalmers (Report, 41) is correct in ascribing a part of this depth to post-glacial faulting.

[8] The depth of the channel to the sea is consistent with this view. The best Admiralty chart (No. 354, "River Petitcodiac and Cumberland Basin") gives the least depth over a rock bottom as 5½ fathoms at extreme low tide, or about 80 feet below high tide. A deeper channel may however exist in the mud or sand on either side of the rock bottom.

[9] An important question arises as to whether this subsidence is still in progress. The evidence is conflicting, and the various students of the subject are not agreed. I believe it is still in progress for these reasons: first, it is still going on in other parts of

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The mode of formation of the marshes.

So much for the origin of the marshes as a whole; we consider next the actual process of marsh-building by the sea. It may best be observed along the tidal rivers, which play an indispensable part in the building of the greater marshes. At ordinary tides the rivers do not overflow their banks nor reach the dikes at all. But at the spring tides every month they rise higher, the waters rush more swiftly, and, gathering up yet more mud from banks and bed,[10] overflow the banks, and, unless stopped by the dikes, spread abroad over the marshes. When the water thus leaves the channels, however, its speed is at once checked, and soon it comes to entire rest: it can no longer carry its burden of mud, and drops most of it. The water leaves the rivers so muddy one can see scarcely an inch or two into it; it returns, a few minues later, fairly clear. The thickness of mud deposited at a single tide varies from a small fraction of an inch on the higher places, to several inches on the bottoms of lakes which have been opened by canals to the tide.

The powerful tidal currents in the crooked rivers cause constant and rapid changes in the soft muddy banks, and all the phenomena of the wandering of rivers in a flood plain may here be seen upon an unusual scale. In fact the marshes are really the flood plains of the tidal rivers, though built by materials

Acadia (as shown in Bulletin of the Natural History Society of New Brunswick 4:339); and second, everywhere outside of the longest-built dikes the marsh is built up higher, even to two feet or more, than it is inside the dikes. Since the marsh was built as high as the tides could reach before it was diked, the land must have sunk to allow it to build so much higher now, even allowing for some sinking of the marsh through the removal of its mineral matters with the crops. Further, the ease with which the tide floods old marsh when admitted, building it up a foot or more, seems explicable only in this way. A case is known on the Tantramar marsh where a large ditch diked upon both sides was neglected, when it filled itself up with mud to a height of two feet above the surrounding marsh.

[10] The percentage of mud in the water is not so great, however, as it appears and as popularly supposed. To the eye it seems often to be little more than "liquid mud." By use of a graduated measuring glass on the end of a long cord I have taken samples from the bridges at various places, which, after settling, allowed the percentage of mud to be determined exactly. I have found the greatest amount in the rivers emptying out at low water, when it rose to an extreme of 4%, and it ranged at other times and places from that downward. At flood tide I have nowhere found it reaching 2%.

carried up their course instead of down. This wandering of the rivers explains many marsh phenomena otherwise very puzzling, such as the occasional miniature cliffs in the high marsh, and the layers of peat or blue mud (both formed only in presence of fresh water away from influence of the tide), exposed by canals, or even by the river itself, which thus reaches places formerly far removed from it.[11]

When the waters spread over the marsh, they of course drop most of their mud, and particularly its coarser parts, on and near the banks, thus building the marsh higher there than elsewhere. Hence the drainage of the fresh water, falling on the marshes as rain or draining upon them from the upland, is obstructed, and it tends to accumulate in the lowest places, viz., those farthest from the rivers, and hence near the upland or in basins between rivers. This fresh water allows the development of a fresh-water vegetation which initiates the formation of true bog, a point of immense importance in the ecology and economics of the marsh-vegetation. Again, at the head of tide in the rivers, the incoming salt water meets the outgoing fresh water and drops its sediment. Thus the rivers are tending always to dam themselves up at the contact of salt and fresh water, and they would doubtless do so completely were it not for the scouring out of the channel by the fresh water when the tide is out. The heads of the rivers, too, show another important phenomenon, viz., the level of high tide is higher there than at their mouths owing to the tendency of tidal rivers to pile up their waters on account of the inertia of their rush.[12] It hence comes about that the marsh is actually higher at the head of a river than at its mouth and the highest part of a marsh is at the

[11] It explains also the presence of concentric lines of old French dikes at Prospect Farm on the Aulac, and probably elsewhere, and the fact that the Misseguash is not now in the same position at Pont à Buot which it has on the very detailed maps of Franquet in 1754. It leads also to the occasional abandonment of pieces of marsh too small to be kept diked profitably.

[12] Mentioned in all works on tidal rivers. I have been told, as a good example of it, that the railroad levels show the high-tide level of the Petitcodiac to be higher at Salisbury than at Moncton; and Dixon and Trueman mention that at the big oxbows on the Tantramar, at very high and rising tides the water pours back over the neck into the river again.

head of the tidal parts of its rivers. This is finely shown by the levels taken on the Misseguash by the engineers of the Marsh Company, of which a condensed compilation is given herewith (*fig. 3*). Where the heads of the rivers wander, as they are particularly liable to do on account of the struggle between the fresh water and the dam at head of tide, a large part of the marsh may be thus elevated at tide-head, and in consequence the drainage above it is greatly obstructed. This results in a great accumulation of fresh water, with a consequent formation of immense bogs; and thus have originated the great bogs at the heads of the Tantramar, Aulac, Misseguash, and LaPlanche.

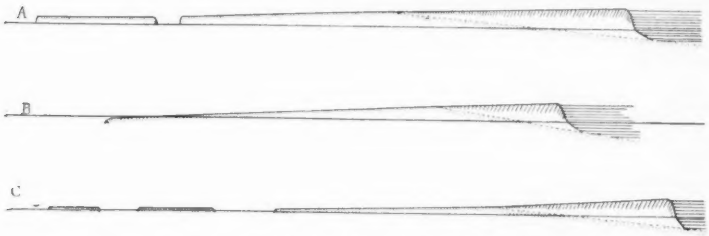

FIG. 3. — True levels on marshes and bogs determined by spirit-level; condensed from the plans of the Misseguash Marsh Co. Marsh is dotted and bog is shaded. The horizontal line is average high water in Cumberland Basin. Breaks in the marsh are where the levels ran along the river. Vertical scale 40 feet = 1 inch; horizontal ½ inch = one mile. *A*, from the Misseguash River near the railroad to Round Lake (*fig. 2*). *B*, from the La Planche River near the railroad to Long Lake; *C*, from Cumberland Basin to Long Lake.

Bogs therefore exist along the margin of upland, between rivers in the same basin,[13] and at the heads of rivers. Their extent, and their position relative to the cultivated and salt marsh may be learned from the accompanying map (*fig. 2*). In a general way the head of tide on the rivers, that is, the highest part of the marsh, marks the transition from marsh to bog; above this point, the rivers are fresh-water streams meandering through bog and expanding here and there into lakes.

The merging of the marsh into bogs is of course very gradual, and it is a well-known fact that the marsh mud extends every-

[13] Of which a perfect example occurs in the "Sunken Island" between the Tantramar and the Aulac (*fig. 2*).

where beneath the bog, even beneath the great bogs at the head of the tidal rivers. Soundings through the bog are easily made, and they show that the depth of the surface of the marsh mud from the top of the bog increases from nothing at the head of tide down to 6 or 7 feet away from the high part. Not enough soundings are available, however, to prove whether or not the slope is gradual from the high marsh to the extreme heads of the bogs, but so far as they go the soundings show this to be in general the case. This is confirmed by the water levels in the canal of the Misseguash Marsh Company. Where the canal

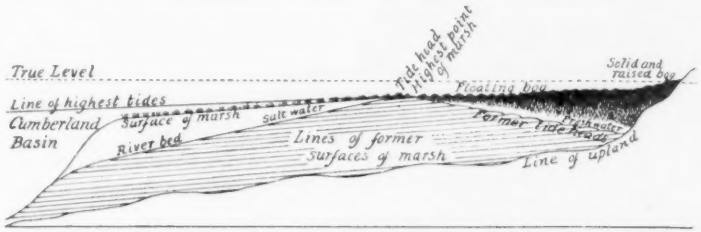

FIG. 4. — Ideal longitudinal section the marshes from sea to upland, to illustrate their origin.

passes through the highest part of the marsh near Black Island, the surface of the mud in July was nearly three feet above the water level; two miles up the bog, however, with a very slight current in the canal, the surface of the mud had dipped under the water, and the slope between the two points was perfectly gradual. It is fair to conclude therefore that the surface of the mud slopes away continuously from tide-head to the extreme distal margin of the bog. The question now arises, why this slope, which carries the bottom of the bog much below high-water level? No doubt the answer is to be found in the subsidence of the land already spoken of. Each part of the under-bog mud must at one time have been the tide-head and the highest part of the marsh; the newer tide-heads would be nearest the present one, and they would be progressively older, and hence have been carried deeper by the subsidence, the farther they are from the present one. This condition is diagrammatically represented in *fig. 4*.

The origin of the great bogs is thus made plain, but why are they mostly of the floating type? They are in fact almost entirely of this kind, though in places they are solid, and even approximate to the raised or *Hochmoor* type. They quake when one walks upon them, and a stick thrust through them penetrates from one to four feet of moss, then goes through a foot or two of water and soft organic mud before reaching the solid marsh mud. The foot or two of water seems to be fairly constant everywhere except in the shallowest parts, while the thickness of the mat of floating moss increases from the shallower towards the deeper parts, as illustrated diagrammatically in *fig. 4*. The levels (*fig. 3*) also show that the surface rises as the bog grows thicker, as is to be expected. It is a general rule in bog-formation over large basins that the floating bog is the first stage, and this is followed, as a result of growth and compacting, by solid bog, which in turn is succeeded by the raised or *Hochmoor* type. It may be a fact, therefore, that the floating character of these bogs is due to their youth — they have not yet had time to form the solid and raised types except on their oldest parts, around the margins and at the heads of the bog rivers, where such types do in fact occur. On this explanation one at first thought attributes the numerous lakes to places which the bog has not yet overgrown. But this explanation is in several respects not satisfactory. The facts seem to show that the growth of bog has been continuous from the upland outward to the marsh. Moreover, the lakes are always deeper than the surrounding bog. It seems, therefore, that there must be some positive factor tending to keep them open.[14]

[14] Possibly it may be connected with the presence in those places of a sufficient supply of salt to prevent the formation of the strongly salt-shy (halophobous) bog vegetation. As the efflorescence of salt on the mud thrown up from deep in the bog by the dredge of the Misseguash Company shows, some salt still exists in the mud beneath the bog water. This must be slowly dissolved out by the bog water, and the solution would settle towards the deepest places, which are the lakes, and might accumulate there to an extent sufficient, when stirred up by the waves, to keep them open of vegetation. The meaning of the deeper places over which the lakes lie is not so plain, but probably they represent in part portions of old river channels. This possible presence of some salt in the bottom water of the bog cannot, of course, explain the floating character of the bog, since the lower layers of vegetation are dead and unaffected by it.

A physiographic fact of some interest about the lakes may here be mentioned.

Economics of the marshes.

I. *Crops and prices.*—When reclaimed from the sea the marshes are wonderfully fertile, and in this respect they are unsurpassed, if they are equaled, by any land in eastern Canada. They are not, however, equally good for all crops, but are best for grasses and grains, to which consequently they are almost entirely given up; root crops will grow upon them, but not to advantage. They form also extremely rich pasturage, and to some extent are used for this purpose. The grasses which grow upon the best parts are the usual upland English hay grasses, which become very tall, very dense, and of very superior quality, luxuriant but not rank, producing easily three tons and upwards of the best hay to the acre. In less well drained places, coarser grasses grow, but these too are of good value. No attempt is made to take two crops a year, though some farmers allow their cattle to fatten on the rich aftermath. No fertilizers of any sort are placed upon the marshes, and the only cultivation consists in an occasional plowing, on an average once in ten to fifteen years, when a single crop of oats is sown, after which the land is brought at once into grass again.

The fertility of the marshes depends upon two, perhaps upon three, features. First there is the presence of the substances and conditions necessary for the perfect nourishment of the crop, as shown by its luxuriance. Second, the fertility is extremely lasting. The best marsh may be cropped with unlimited yield for decades together without any return to the soil. There are places on the Aulac, which are known absolutely not to have been renovated in any way since 1827, and are believed not to have been treated in any way for fifty and perhaps a hundred and fifty years before that, which are bearing today crops as bountiful as ever. There is on this river, at Prospect farm, a small triangle, known not to have been even plowed for over forty years, which has never ceased to bear a luxuriant crop of the best English hay grasses. These are of course among the

Some of them are in contact, particularly on their northeastern margins with the uplands and have there gravelly beaches. This is no doubt correlated with the prevalence of strong southwest winds in the region, which cause a surf on the northeast shores unfavorable to the development of bog vegetation.

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best places; but there are parts, particularly on the marsh longest reclaimed, which show more or less exhaustion.[15] Such marsh may have its fertility largely restored by fresh mud brought in by the sea when allowed behind the dikes. Third, the water conditions of the marsh soil are such that the vegetation is somewhat less affected by dry seasons than is that of the uplands, and a bad hay year for the uplands is not so bad for the marshes. The causes of all these peculiarities in the marsh fertility will be discussed later.

The result of this combination of good qualities is, naturally, to give the marshes a high value. Marsh situated near the towns, and well-placed for drainage, is worth upwards of $180.00 to $200.00 per acre; there are large areas valued at $100.00 an acre, while prices range, of course, from these downwards.

II. *Mode of reclaiming the marshes.*—The original marsh as built by the sea bears a sparse vegetation of typical salt marsh plants, of which only a few of the grasses, and these to a limited extent, are useful. To reclaim this marsh three things are needed: (1) to shut out the sea, (2) to wash out most of the salt, (3) to provide for the removal of the fresh water falling as rain or draining from the upland. The sea is shut out by dikes of the usual sort. These are triangular in section, built of the marsh mud itself, often with a core of stakes and brush. Against the open sea they may be six feet high, and they are protected from the wash of the waves by lines of stakes or piling and loose stones; but along the rivers they are much lower, for up the rivers the marsh itself is progressively higher. The removal of the salt takes place naturally by action of the falling rain, which washes it through the drains into the sea. It requires three to four years in newly reclaimed marsh to do this sufficiently to allow the more useful grasses to grow, and during this time there is an entirely natural succession of plants accompanying the freshening, whose kinds and sequences will presently be discussed. To allow the rain-water to drain off is all-important, not only for removal of the salt and for proper aeration of

[15] This is not to be confused with degeneration through bog-formation on account of defective drainage, a common but morphologically very different phenomenon.

the soil, but also to prevent the ever-present tendency to formation of bog plants. This drainage is accomplished by a system of open ditches, which, small and only a foot or two deep away from the rivers, are much larger and deeper near them, partly to give a fall and partly because of the greater height of the marsh there. At the outlets of these ditches on the rivers the fresh water is allowed to drain out by an arrangement that does not allow the tide to enter, namely, by placing under the dike a wooden "sluice" in which hangs a "clapper," hinged at the top and inclining outwards toward the river at the bottom (*fig. 5*). When the tide is out, the pressure of the fresh water

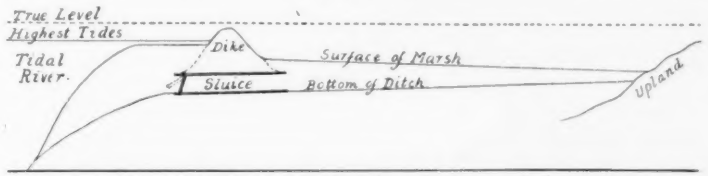


FIG. 5. — Diagrammatic cross-section through the marsh from tidal river to upland, showing a sluice.

opens this; when the tide rises its weight tightly closes it. Of course the fresh water then accumulates in the ditches, but never for long, for the sluice is not far below high-water mark. These sluices and clappers last indefinitely, apparently preserved by some antiseptic action of the salt water. A sluice of this kind is used not only in the ditches but frequently in a dike thrown across an entire river, as in the case of the Aulac. The entire structure, dike and sluice, is then called an "aboideau," and such a river is said to be "aboideaued."[16]

[16] A word introduced by the Acadians from Saintonge, France, where it is still used in the form *aboteau*. Its origin is fully discussed in the New Brunswick Magazine 1 : 225, 226, 284, 340, and 3 : 218. Naturally some other peculiar uses of words have grown up in the marsh country. Thus, the word tide is used for the salt water itself, and one often hears "let the tide on the marsh." Also the word is used constantly as a verb, as "They intend to tide the marsh," *i. e.*, to let the salt water on it, and "It was tided last year." The word ditch is used also as a verb. A large section of marsh surrounded by a single dike is called "a body." In Nova Scotia, the word dike is applied to the marsh itself (no doubt abbreviated from "diked land"), while the dike is called the "running dike," but the usage in New Brunswick is as in this paper. The word *marsh* itself is rather a misnomer and is said locally to do the country some damage by giving an unfavorable impression of its character.

The process of flooding a piece of land that has degenerated through cropping, or through bog growth as a consequence of neglect of drainage, is simple. The dikes are broken down at convenient places, and the tide is allowed to flow at will over the old marsh. Bog vegetation is killed immediately by the salt water, and it, as well as the entire marsh surface, is soon covered with several inches to a foot, or even more, of new mud. This requires from one to three years according to the situation of the marsh.[17] The dikes are then rebuilt, ditches are opened, the vegetation goes through its usual cycle, and in from two to four years it is again bearing rich English hay. This flooding, however, is by no means as extensively used as it should be, for many owners are unwilling, or cannot afford, to lose all return from their land for several years. Sometimes an attempt is made to flood and obtain crops simultaneously, by admitting only a little tide at a time, or by admitting it only in late autumn after the ground is frozen, when the grasses are little injured by it. But such compromises are considered not to pay in the end.

The struggle with the fresh water is incessant, and is the greatest care and expense of the marsh farmer. Poor drainage soon leads to the replacement of the valuable English hay by the less valuable sorts, which in turn yield to yet coarser kinds, the series ending in the appearance of useless sphagnum mosses and bog plants. Abundant and intelligent ditching is the only remedy. Farmers differ so much, however, in willingness or ability to face this problem, that areas alongside of one another under similar natural conditions with but a ditch between differ greatly, one bearing the richest English hay, and the other only the coarser kinds.[18]

[17] It seems remarkable that no attempt has been made to hasten this process by utilization of the powerful currents of the rivers to turn wheels which could pump the water and mud upon the land. Such wheels are used in other countries for irrigation purposes.

[18] There is, however, another difficulty, much more serious, which greatly hampers both the struggle with the bog and the renovation of old and exhausted marsh. The dikes are built and maintained at the common expense of a large number of owners of marsh land, and enclose a huge "body" of marsh. Owing to differences of location and of treatment, some parts of such a body come to need tiding while others do not, and

So much for the reclamation and renovation of the marshes. In addition there has grown up within a century a most important practice of reclaiming and converting into marsh both the lakes in the bogs and the bogs themselves. Its principle is simple, though the practice is by no means so. Canals are dug from the tidal rivers into the lakes, whereby the latter are drained and the tide is allowed to enter with the rich mud. In this way a lake may be entirely filled with mud and become the richest of marsh, and this has been done in the several lakes shown by the red lines on the detailed map (*fig. 2*). After the lakes have been thus reclaimed, the surrounding bog is attacked. The salt water turned upon the bog kills at once all vegetation, which compacts, sinks, becomes covered with marsh mud and gradually comes into rich marsh. Immense areas have thus been reclaimed on the Tantramar system, as shown upon the map above cited, and the process is steadily going on, while a systematic attempt is being made by the Misseguash Marsh Company to reclaim on a large scale the lakes and bogs on the Misseguash. In such operations the most constant care is needful to prevent the canals from damming and filling themselves up, and this is mainly accomplished by utilizing the outward rush of the fresh water to scour out the channels. The great aim, therefore, is to secure the greatest possible "rush of tide up, and of freshet down." There are marsh farmers who have become very expert in lake and bog reclamation, to their own profit and the good of the community. I believe this process of reclaiming bog, here practiced, is entirely unique.[19]

An important feature of the economics of the marshes is the aboideaued rivers, already explained, of which the Aulac is by

there are all gradations between. Disputes then arise among the owners of the body as to the course to be pursued, which often go so far that nothing at all is done, and great stretches of marsh suffer so severely as to become of little value. This is most markedly the case on parts of the Shepody marshes, large areas of which, capable of the highest development, are lying nearly ruined through the inability of the owners to co-operate for the common good. It would seem proper for the local legislature to interfere in such cases, where not only the interests of some owners are concerned, but also the prosperity of the neighboring region.

[19] The process is more fully described in the papers by Crawley, by Goodwin, and by Trueman, cited in the bibliography.

far the best example. An aboideau, shutting out the tide while allowing drainage of fresh water, recovers at one operation, without the expense of river-dikes, all the marsh along the river above it, and also the banks of the river and much of its bed, both of which, but especially the banks, produce the very richest of hay. At first sight it might seem wise to aboideau all rivers at their mouths, but when it is remembered that no land above the aboideau can be renewed by the tide, nor can any bog or lake be reclaimed, it will be seen that an aboideau is only profitable on streams which have no bog nor lake at their heads, and which have a soil so deep as not to need renewal. This is true of many smaller streams heading against upland, but of none of the rivers excepting the main Aulac. An aboideau upon the Tantramar would have prevented the reclamation of thousands of acres which are now productive. Naturally, therefore, there is much jealousy of aboideaus upon the part of those who own inferior marsh or bog above them, and the words of a local writer,[20] who calls them "the curse of our rivers," reflect a common opinion.[21]

[20] MR. WM. FAWCETT, of Upper Sackville, in newspaper articles.

[21] The marshes were first reclaimed by the Acadian French, who began the work in 1670 and continued it, raising much grain, until expelled by the English in 1755. They developed the methods of reclamation (of marsh, but not of bog) still in use, and many of their old dikes are still to be seen. The extent of their operations is well shown upon several maps of the time (particularly on "A large and particular Plan of Chignecto Bay," 1755), and its limits are marked by the fine dotted line drawn on the accompanying detailed map (*fig. 2*). The lands lay vacant from 1755 to 1760, after which they were regranted to New Englanders and English, and their settlement and reclamation has continued steadily to this day. In 1827 the Aulac was first successfully aboideaued, as were later the Misseguash and the La Planche, though from both of the latter the aboideaus have since been removed. No attempt was made to reclaim bog and lake until early in the last century, when a farmer of Upper Sackville, Toler Thompson, whose name is justly held in high honor in the vicinity, after long study of the tidal currents and bog levels became convinced that the lakes could be filled and reclaimed. It was long before others could be convinced, but finally a canal was dug from the Tantramar into Rush Lake (*fig. 2*) which quickly became rich marsh. Later Goose Lake was recovered, and later Log Lake (which required fifteen years to fill with mud), while Long Lake, Ogdens and others are now being filled, and thus the system initiated by Thompson is adding immensely to the wealth of this region. On the Misseguash little had been done, but five years ago a company "The Misseguash Marsh Company" was organized to attempt to do with ample capital, systematic methods, and favorable legislation, what had been done piecemeal

One other phase of the economics of the marshes remains to be mentioned. They are absolutely healthful. No malaria nor other disease is known about them. There is a local tradition that men have died from drinking the bog water; but I am told by a local physician that cases of typhoid fever are referred to and that these were probably contracted in quite another way.

The importance of the ecological study of the marsh vegetation.

From a systematic or floristic point of view these marshes are of slight botanical interest. They contain no species that are peculiar to them, out of range, or otherwise remarkable. The plants of the unreclaimed marshes, and also of the bogs, are those ordinarily occupying such situations in this part of America, while the fully reclaimed marsh is but a good hay meadow, bearing grasses altogether like those abounding on the cultivated uplands round about. Yet from another, namely, the ecological point of view, the marsh vegetation is replete with scientific interest, for the marked gradations of physical conditions of soil and water within a limited space, and, owing to artificial changes, within a limited time, allow us a rare chance to trace upon a large scale the effects of those important conditions upon the plants, and to draw some conclusions as to the nature of the adaptation of the one to the other. It is necessary, first of all, to study carefully these, and other, physical factors to which the plants must respond; then we may trace the responses in the plants.

The factors determining the ecological features of the marsh vegetation.

The principal ecological factors, as arranged in Schimper's comprehensive work, *Pflanzengeographie auf physiologischer Grundlage*, are the following: *Water*, *temperature*, *light*, *air*, *soil*, *animals*

on the Tantramar. This company is now vigorously at work, and it is hoped that their efforts to convert the thousands of acres of useless bog on this river into productive marsh will be entirely successful.

The best account of Toler Thompson and his work that I have seen is in an article by Judge Botsford in the *Chignecto Post* in January, 1886. Another valuable article on the history of marsh reclamation is that by Mr. Howard Trueman in the *St. John Sun* in late December, 1897.

(including the aggressive *man*). To these should be added another of great importance, *geography of the basin.*

Water.—Of all the factors determining plant form and distribution, this is the most important. We consider first the precipitation of the marsh country. No records are available for the immediate vicinity, but it may be inferred from the amount in places surrounding the region. Thus, according to the rainfall map published in 1899 to illustrate the presidential address (by T. C. Keefer) before the Royal Society of Canada, the mean annual rainfall is: at Moncton, N. B., 44.96^{in}; at Truro, N. S., 43.28; at Charlottetown, P. E. I, 41.45, while at St. John, N. B., it is 47.38^{in}. The marsh country, lying at the head of the Bay of Fundy, and directly in line with it, probably has less rainfall than St. John, but more than any of the other localities; and hence we may fix it conservatively at 45^{in}.

As to its distribution through the year, the only available records are for St. John, where it is as shown in the following table, "for a long series of years," supplied to me by the Dominion Meteorological office at Ottawa:

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
5.55	3.93	3.80	2.50	3.66	2.72	3.29	4.64	3.08	4.13	4.71	5.16	47.17^{in}

Diminished *pro rata* for the lesser total rainfall, this table represents proportionally, no doubt, the distribution of precipitation through the year at the marshes.

It thus appears that the marshes have a precipitation ample for the development of an abundant temperate-region vegetation, and that it is distributed fairly evenly through the growing season of the year.

As to prevailing humidity of the atmosphere, there are no records available even at St. John. But since there is much cloudy weather, no little fog and mist, almost insular conditions, and very constant southwest winds blowing over the entire length of the Bay of Fundy, the humidity must be rather high.

Turning to the influence of water in another way, its mechanical effects, several points are to be noted. One is the very impor-

tant result arising from the abundant precipitation in connection with the poor drainage, leading to the formation of the immense bogs later to be considered. The presence of ground water in soil is usually important, but it here plays little or no part, as will be pointed out later. Another effect is in the scattering of seeds by means of currents. It would seem that the tidal currents in the rivers must form efficient disseminators of the seeds of at least the salt-plants. I have made a test of this by bringing back from the marshes several samples of the newly-deposited marsh mud, which the next spring were given very favorable conditions for the germination of any seeds in them, but no plants appeared. It may be that none were present in summer, and autumn samples might give a different result. There is, however, another mechanical effect of the tidal currents of considerable importance, namely, although they have built up the marshes entirely, they keep the river banks so constantly shifting, laying down mud in some places and scouring it out in others, that no vegetation is able to gain a foothold below the quieter zone near high-tide marks, excepting in the case of the curious sedge bogs, which I do not entirely understand; and these great banks are bare of all plant life excepting an occasional diatom swept from the sea. These banks and flats must be the largest areas barren of life in all northeastern America.

Temperature.—Next in importance to moisture as an ecological factor, is temperature. I have been unable to secure a copy

	January	February	March	April	May	June	July
Mean highest	28.2	27.6	34.3	46.4	57.2	64.4	68.8
Mean lowest	9.0	9.7	18.3	30.8	40.4	48.3	53.2
Mean temperature	18.6	18.7	26.3	38.6	48.8	56.3	61.0
Mean daily range	19.2	17.9	16.0	15.6	16.8	16.1	15.6
Absolute highest	50.0	49.0	52.0	71.7	75.0	86.7	88.9
Absolute lowest	−21.0	−15.0	−10.0	12.0	27.0	35.0	41.0

	August	September	October	November	December	Year
Mean highest	68.8	63.3	51.8	43.3	32.4	48.9
Mean lowest	53.7	47.8	37.6	28.9	15.1	32.7
Mean temperature	61.3	55.6	44.7	36.1	23.7	40.8
Mean daily range	15.1	15.5	14.2	14.4	17.3	16.2
Absolute highest	85.0	85.0	72.4	61.0	54.5	88.9
Absolute lowest	43.0	32.5	21.4	− 1.5	−19.5	−21.0

of the records kept in Sackville in the marsh country, and must turn therefore to those of St. John. The above table, based on the averages for a long series of years, is supplied by the Dominion Meteorological Office at Ottawa. Owing to well-known local conditions, the summer temperatures average lower, and the winter higher at St. John than elsewhere in the province, and this correction must be applied to the table to make it of use in estimating the conditions of the marsh country.

It is important to note further, that on the marshes themselves the snowfall is said not to be great, and often for considerable periods in winter the ground is bare. This condition, combined with the strong winds that prevail there and the total lack of shelter on the marshes, makes the winter conditions unusually unfavorable for vegetation, which must consist of plants able to endure such trying conditions. For this no arrangement is better than that of the grasses, which largely retreat to or under the ground in winter. On the other hand, at times in summer, the marshes, lying at sea level and completely unshaded, receive so strong an insolation as to become very hot, though this is never long continued.

Light.—The latitude of these marshes is 45° 50′ to 46°, from which the amount of light they would receive if unshaded by clouds, etc., and with a clear atmosphere may be estimated. But the full amount is much diminished by cloudy weather. No records of cloudiness are kept nearer than St. John, where the percentages for a long series of years are as follows:

Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
53	54	60	55	61	62	63	62	53	58	60	59	58

Probably the cloud percentage for the marshes is not very different from this, though it would be less rather than more, say 50 per cent. for the year, 55–60 per cent. for the summer months. No records whatever for intensity of the light are available. It is important to note, however, that the marshes, perfectly level and unshaded, receive the full value of what light there is.

Air.—Here as elsewhere, chemically the air is hardly an ecological factor; at all events it is not a differential factor. Atmospheric pressure on the marshes, lying at sea level, is of course at its maximum, but the daily fluctuations of the barometer, as Schimper remarks, have no known effects upon the form or distribution of vegetation. Mechanically, however, as it moves in winds, the atmosphere is here important. Unfortunately no official meteorological records are available for direction or velocity, but a record of another kind is visible and unmistakable, namely, the wind effects upon the vegetation. As I have elsewhere pointed out,[22] the trees and shrubs on the neighboring ridges and in places on the margins of the bogs are strongly bent to the northeast, and show a great development of branches on that side, with an abortion on the southwest. This is caused by the very strong southwest winds which prevail here, as the residents agree, during most of the year, a phenomenon resulting from the position of the marshes in relation to the Bay of Fundy. This great bay lies northeast and southwest, and is of the form of a huge funnel. Wide at its mouth, it narrows between walls of increasing height (300 to 700 feet or more) towards its head. At Cape Chignecto the northern branch, with which we are concerned, continues and even intensifies this funnel character, ending finally in the low-lying marsh country. The great winds here are due to very much the same causes as the great tides. Every wind from a southerly direction is thus brought into a southwesterly course, condensed, strengthened, and poured over the low-lying marsh country, and the vegetation must be of a kind to endure it, for which nothing is better than the grasses.

It might be expected, as a result of the prevalence of these winds, that dunes would be formed on the unreclaimed marshes. There is, however, not the least trace of this, chiefly because the mud when laid down by the tide hardens as it dries, allowing the wind no hold upon it.

The constancy and strength of the winds on the marshes must greatly promote evaporation (transpiration) from any

[22] Bull. Nat. Hist. Soc. New Bruns. 4: 134.

vegetation there, not only in the summer, when an abundance of water is usually available for the vegetation, but in those critical periods of winter and early spring, when, owing to the low temperature of the soil, water is not readily absorbed.

Another important influence of wind upon vegetation consists in its effects upon cross-pollination and dissemination. Obviously the conditions are particularly favorable for wind-pollination on the marshes (and by that very fact somewhat unfavorable for insect-pollination), and the same is true for wind dissemination. We shall see later how much the vegetation is influenced by these factors.

[*To be continued.*]

GEOGRAPHIC DISTRIBUTION OF ISOETES SACCHARATA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LI.

GEORGE HARRISON SHULL.

(WITH MAP)

WHILE making a study of the aquatic vegetation of Chesapeake Bay for the U. S. Bureau of Plant Industry during the summer of 1902, I located several new stations for *Isoetes saccharata* Engelm. This species has had an interesting history, and as our knowledge of its range has greatly increased within the last few years, I have thought it desirable to publish the accompanying map showing the exact distribution as now known, to give a detailed account of its history, and to discuss briefly several problems which have presented themselves for solution.

For a quarter of a century *Isoetes saccharata* Engelm. was known only from its type locality on the Wicomico River and from the Nanticoke, which empty into the bay by a common mouth opposite and a little north of the mouth of the Potomac. Far up the Wicomico, about a mile below the town of Salisbury, Maryland, the plant was first discovered by William M. Canby in 1863. The material was submitted to Dr. Engelmann, who was at that time the highest American authority on the genus, and was first described by him in Gray's *Manual*, 5th edition, p. 676, 1867. In 1874 Canby found a second station at Seaford, Del. Not until 1888 was it collected at a third station, when it was found by Vasey and Coville near Alexandria, Va., in Hunting Creek, a tributary to the Potomac. The material obtained here was not recognized for some years as identical with Canby's material, and was referred by Theo. Holm to *Isoetes riparia* Engelm.[1] The next year Coville found it at Mount Vernon on the Potomac, but this collection seems to have been overlooked

[1] Proc. Biol. Soc. Washington 7: 132. 8 Ap 1892.

by Holm, and was not published until in 1900, when it was mentioned in the *Sixth List of Additions to the Flora of Washington*.[2]

Not until 1893 were specimens recognized as *Isoetes saccharata* Engelm. secured away from Canby's stations on the Wicomico and Nanticoke Rivers. In this year T. Chalkley Palmer discovered it near the western end of the Delaware and Chesapeake Canal in Back Creek, a tributary to Elk River, nearly 140^{km} north of the type locality. During the next two years he discovered it at several other points in both Elk and Sassafras Rivers. These collections formed the subject of an interesting account published in the BOTANICAL GAZETTE in 1896.[3]

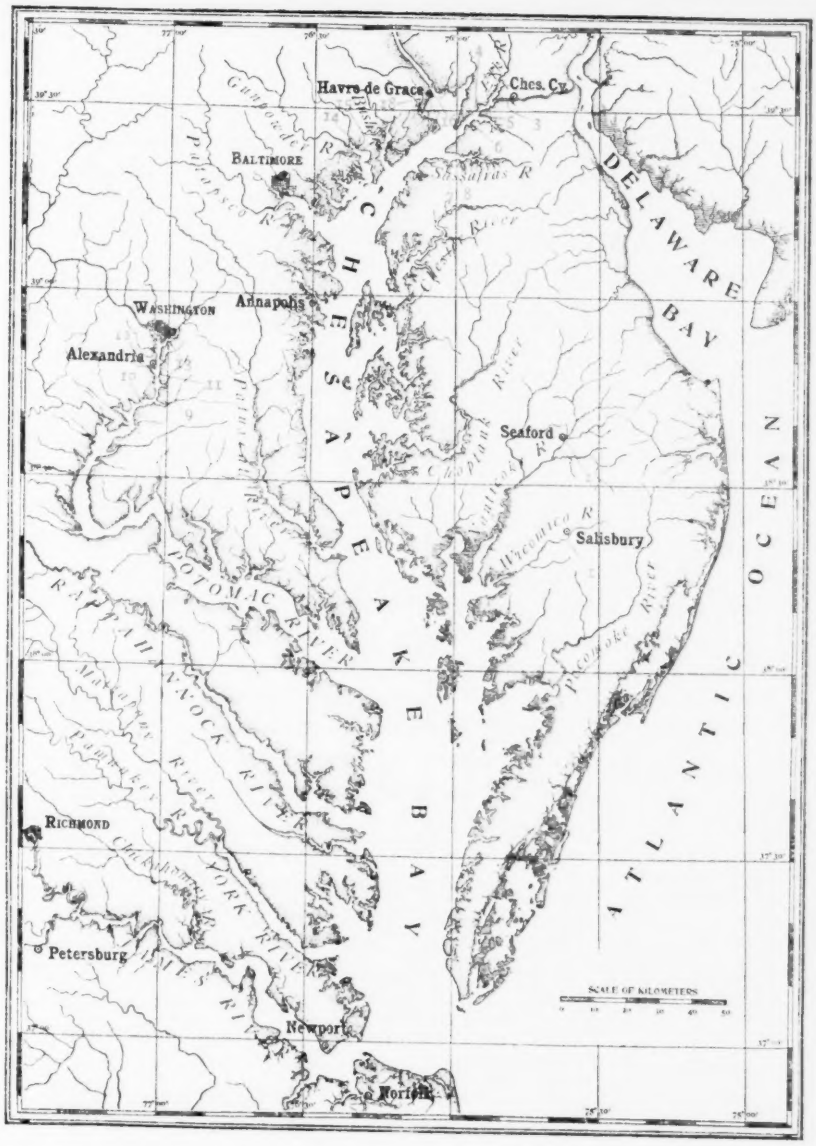
The only new stations which have been published since Palmer's account are given in the *Sixth List of Additions to the Flora of Washington*,[4] where, besides the reference to Coville's Mount Vernon station above mentioned, two new localities are recorded for the upper Potomac. Along with the publication of these stations were given the descriptions of two new varieties: var. *Palmeri* A. A. Eaton, based upon Palmer's material from Lloyds Creek, Sassafras River; and var. *reticulata* A. A. Eaton, based upon several collections, including that of Vasey and Coville (1888) from the Hunting Creek station, Alexandria, Va.

Since the publication of Palmer's paper on Isoetes, that collector has located several new stations which are here published for the first time. The most notable of these, and the only one outside of the Elk and Sassafras Rivers, is about 25^{m} north of the Havre de Grace light at the mouth of the Susquehanna River, and therefore at the very head of the bay.

I believe these are all the localities known for the species before my collections of the past summer. My work was limited almost entirely to the west side of the bay, and my collections of *Isoetes saccharata* were made in the western tributaries and along the shore of the northern part of the bay, my most northern station being only 500^{m} from Palmer's Havre de Grace station, thus making the circuit about the head of the bay virtually complete.

[2] Proc. Biol. Soc. Washington **14**: 49. 19 Je 1901.

[3] BOT. GAZ. **21**: 218–223. 1896. [4] *Loc. cit.*



EXPLANATION OF MAP OF CHESAPEAKE BAY.—Adapted from Coast Chart number 376 of U. S. Coast and Geodetic Survey, and McGee's Drainage Map of the Middle Atlantic Slope (U. S. Geol. Survey, Seventh Annual Report, *pl.* 57.) Stations for *Isoetes saccharata* Engelm. are located at the points in which the index lines cut the shore lines.

So far as could be determined, the index lines are perpendicular to the portion of the shore occupied by the Isoetes.

It will be seen then that within the last ten years *Isoetes saccharata* and its forms have been traced from its original station completely to the head of the bay. Wicomico River is yet the most southern station known, but it is not improbable that a careful exploration will result in its discovery in the fresh-water estuarine portions of the more southern tributaries of the bay.

For the sake of completeness and to facilitate further study of the several colonies now known, as well as to serve as an index to the map, I insert the following list comprising all the known stations, with such data as I have been able to gather regarding each. The figure preceding each name agrees with the corresponding station as indicated on the map. In each case the station is at the point in which the index line intersects the shore line.

1. *Salisbury, Md.*—On a label in the herbarium of G. Engelmann, St. Louis, Mo., now in the Missouri Botanical Garden, the type locality is described thus:[5] "Shores of Wicomico River, one mile [1.6^{km}] below the town of Salisbury, eastern shore of Maryland, on gravel, covered by a thin layer of mud deposited by the tide; alternately covered and exposed by the tide. . . . . Growing in the society of *Sagittaria pusilla* (*S. subulata* [L.] Buchenau), *Tillaea simplex* (*T. aquatica* L.), *Hemianthus micranthemoides* (*Micranthemum micranthemoides* [Nutt.] Wettst.) etc.; first found Sept. 15, 1863. Wm. M. Canby." This label, which bears the date September 8, 1866, evidently belongs to a type specimen. In a letter to the writer, Canby explains that the original station is a sandy or gravelly slope on the south side of the river.

In September 1895 T. C. Palmer, in an attempt to visit the type locality, found the species growing at Williams Point on the Wicomico River.

2. *Seaford, Del.*, is situated at the confluence of the north and south branches of the Nanticoke River, and only 5^{km} below the head of tide water. A label in the Engelmann herbarium,

[5] A similar but somewhat ambiguous description of the type locality occurs in Engelmann's paper on "The Genus Isoetes in North America." Trans. St. Louis Acad. Sci. **4**: 382. 1882.

belonging to one of the original specimens from this station reads: "Muddy and gravelly shores of Nanticoke River near Seaford, Delaware. Wm. M. Canby, Wilmington, Del., August 1874." That this was the first collection at this station is shown by the fact that duplicates in the U. S. National Herbarium and in the Herbarium of the Field Columbian Museum bear the statement that it is "a new station." The area occupied by Isoetes at this place is located "nearly opposite the town, a little above it, in fact. The space there is not very large, perhaps 100[ft]"[6] (30[m]).

3. *Back Creek*, tributary to Elk River, eastern shore of Maryland. This station is on the south shore of the creek about 3[km] from the western end of Chesapeake and Delaware Canal and nearly 1[km] below Chesapeake City. The first collection was made by T. C. Palmer in August 1893. He made further collections the following year and published a short statement in the BOTANICAL GAZETTE.[7]

4. *Piney Creek Cove* is a broad indentation in the north shore of Elk River 9–11[km] from its mouth. On August 13, 1894, T. C. Palmer collected *Isoetes saccharata*, just below the mouth of the small stream which empties at the northeast angle of the cove. This station was also mentioned with the last in the BOTANICAL GAZETTE.

5. *Town Point* is the upper angle formed by the confluence of Bohemia River with Elk River, into which it flows from the east. About 500[m] north of this point Isoetes was collected on July 31, 1896, by T. C. Palmer. A specimen from this collection in the National Herbarium gives the habitat: "Tidal tract; gravel nearly bare." This station has not been previously recorded.

6. *Cabin Johns Creek* empties into Elk River from the southeast about 5[km] above the mouth of the latter. A specimen in the National Herbarium bears the data: "July 21, 1896. Cabin John's Creek, Elk River. Tidal tract; gravel covered with mud. Collector T. Chalkley Palmer." This collection has not been published heretofore.

7. *Lloyds Creek* is a large shallow cove on the south shore of

[6] William M. Canby, in a letter. [7] BOT. GAZ. **20**: 32. 1895.

the Sassafras River, about 6[km] east of Howells Point, and is nearly cut off from the river by a sand spit. On the south shore of this shallow bay, almost due south of its mouth, a very interesting collection of Isoetes was made by T. C. Palmer, August 12, 1895. The habitat as described on a label in the National Herbarium is characterized by "reddish sand capped lightly with mud." The material departed in a marked degree from typical *I. saccharata* Engelm., as was pointed out in the collector's interesting contribution in the BOTANICAL GAZETTE in 1896 (*l. c.*). In 1900, A. A. Eaton made this material the basis of his new variety *I. saccharata Palmeri*. In a letter to the writer, Palmer states that at none of his other stations does the Isoetes grow in such abundance as at Lloyds Creek.

8. *Turners Creek* empties into Sassafras River from the south about 4[km] east of Lloyds Creek. On the south shore of Sassafras River just below the mouth of Turners Creek, a station, published here for the first time, was located by T. C. Palmer, July 18, 1897.

9. *Hunting Creek* empties into the Potomac River from the west immediately south of the city of Alexandria, Va. The highway from Alexandria to Mount Vernon is graded for some distance into the shallow part of the creek from each side, and crosses the middle part by a long bridge. The original station is a gravelly bed near the bridge on the right side of the embankment as the bridge is approached from the Alexandria end. The first collection at this place was made by George Vasey and F. V. Coville, July 22, 1888. It has been visited several times since, a recorded visit[8] having been made by W. R. Maxon, September 22, 1900. Maxon also collected at this station, September 7, 1901, a specimen of this date being placed in the National Herbarium. The writer secured specimens from the same place August 11, 1902, and also found it on the same side of the embankment which leads from the opposite end of the bridge toward Mount Vernon. These areas are not large, but the material is fairly abundant. The soil consists of pebbles covered with a layer of mud and the principal companion plant

[8] Sixth List of Additions to the Flora of Washington. *Loc. cit.*

is *Eriocaulon septangulare* With. The material collected at the Alexandria end of the bridge by Vasey and Coville, and Maxon's 1900 collection along with Steele's Anacostia material, soon to be mentioned, were made the basis of the new var. *reticulata* A. A. Eaton.

10. *Mount Vernon, Va.*, is on the west bank of the Potomac about 11 km south of Alexandria, Va. A specimen in the National Herbarium, collected at this place, bears the data: "Mt. Vernon, Va., July 4, 1889. Shore of the Potomac at the foot of the Mt. Vernon estate, Collector F. V. Coville." The collector describes (*in litt.*) the station as being "at the slope immediately in front of the house and therefore a hundred yards or more (100 m) north of the boat landing. There was a considerable area here in shallow water covered with Isoetes. The soil was gravelly."

11. *Notley Hall, Md.*, is on the east shore of the Potomac River, nearly opposite the mouth of Hunting Creek, Alexandria, Va. A specimen in the National Herbarium was collected at this place by F. V. Coville in 1894.

12. *Four Mile Run, Va.*—This creek enters the Potomac from the west about midway between Washington, D. C., and Alexandria, Va. Its lower course forms a wide bay, along the south side of which the banks are being eroded by wave action, which carries away the finer material, leaving a gently sloping tide-beach of mingled sand and gravel, on which Isoetes grows luxuriantly. The first collection at this station was made by E. S. Steele, August 5, 1898. The writer visited this place and made collections on August 22, 1902.

13. *Anacostia River* crosses the District of Columbia east of Washington, D. C., and empties into the Potomac River just south of that city. On September 1, 1900, E. S. Steele discovered Isoetes "on the southeast bank of the Anacostia River nearly opposite the Navy Yard, perhaps a half [one-fourth] mile below the Navy Yard bridge."[9] This collection forms a part of the type material of var. *reticulata* A. A. Eaton.

14. *Sugar Loaf Creek* is a small stream which empties into Gunpowder River, western shore of Maryland, from the north,

[9] In a letter to the writer.

at a point about 600[m] northeast of Gunpowder station on the P. B. & W. R. R. On the small rounded point between Sugar Loaf Creek and Gunpowder River, I found *Isoetes saccharata* on September 2, 1902. The specimens were abundant but of small size, owing to the fact that they grew in a moderately dense colony of *Scirpus americanus* Pers., among which I have rarely found Isoetes elsewhere. Other associates of Isoetes at this station were *Lilaeopsis lineata* (Mx.) Greene, and *Eriocaulon septangulare* With. The soil conditions were typical—gravel covered with a thin layer of mud.

15. About 500[m] above the mouth of Sugar Loaf Creek, on the east shore of Gunpowder River, I located another colony of Isoetes the following day, September 3, 1902. The specimens at this place were growing in a bed of sand only a few square meters in extent and were very thrifty.

16. *Havre de Grace Light* is on a small point on the west shore of the Susquehanna River at its mouth. The most interesting of T. C. Palmer's unpublished stations for Isoetes is a small area just north of this light house, near the pier. His collection at this point was made August 17, 1898, and is at present the northern known limit of the species.

17. *Havre de Grace Park* is along the shore of the bay, southwest of the Havre de Grace light. It descends to the bay by a steep bank, and below this bank, among the pebbles which pave the beach, I found the species growing abundantly, July 19, 1902.

18. Nearly 1[km] west of the last, on the curved shore, known as the "knee" of the bay, *Isoetes saccharata* also grows, though not in such abundance as at the park station. I collected at this place also July 19, 1902, this being my first collection.

x. By this sign I have marked two points on Bush River at which single small specimens were found. The fact that these two specimens were seen indicates that its absence in notable quantity is due to unfavorable habitat, and not to barriers to its entrance. Although Bush River was explored from its mouth almost to the head of tide water, I did not see a single spot where I really expected to find it. The specimens found were evidently

choked by the density of the *Scirpus americanus* Pers., among which they grew. Where the shores were free from Scirpus, as they were for stretches north of Bush River station, P. B. & W. R. R., and at the mouth of Otter Creek, they were composed of pure gravel, subject to shifting with the action of the waves.

y. I have indicated thus the location of a well-grown specimen found floating in the bay at the mouth of Furnace Creek over 3 km from the nearest known colony.

It appears from this list of known stations that *Isoetes saccharata* has a general distribution in the fresh water portions of Chesapeake Bay and its tributaries, but is at present unknown from any other locality. If it has a wider distribution, our ignorance of that fact is not entirely due to lack of observation, for Delaware Bay, which furnishes the most accessible suitable habitats, has been explored by students of the genus, with the result that several stations have been located for *Isoetes riparia* Engelm., but not a single specimen of *I. saccharata* Engelm. has been found.

If the last named species is indeed limited to Chesapeake Bay, it will be of interest to consider the causes to which the restriction may be due. Endemic species have a peculiar interest in their bearing upon problems of biogeography. A cosmopolitan distribution is evidence of a high degree of adaptability to variation of habitat, and is also evidence either of an old species or of efficient means of dispersal. On the other hand, a species which is limited to a single locality is either a remnant of a once more widely distributed form, or it is a relatively new species which has arisen in the more or less isolated region to which it is now limited. In the first instance it has been protected by the barriers which surround it, or by peculiarly favorable conditions for its growth from the extinction which has overtaken the species in other regions; in the second case it has been prevented by barriers from spreading beyond the region of its origin. Cosmopolitan species seem to deny the existence of barriers, while local species not only confirm their existence but give a clue to the nature and position of these barriers. As biogeography has to do preeminently with barriers, it is evident

that species of local range are of the greatest importance in solving the fundamental problems of geographic distribution.

From this brief discussion it will be seen that there are two essentially different kinds of endemism. In one the species is a remnant, in the other it is a beginning. To the former of these the term *relict* endemism has been applied;[10] to the latter I shall apply the term *initial* endemism.[11] Relict endemism is illustrated by such classic examples as the Sequoia of western North America and *Ginkgo biloba* L. of eastern Asia. Initial endemism is perhaps best exemplified by numerous endemic species of oceanic islands, though it does not follow that all endemic species of oceanic islands are initial.

It is obvious that many difficulties will be encountered in determining whether any local species in question is a relict or an autochthon. It is also obvious that we may have initial species of a relict genus, though not the reverse. After examining the nature of the barriers which limit the distribution of *Isoetes saccharata* I shall suggest to which class of endemic species it probably belongs.

It will have been noted in examining the map, or in looking over the descriptions of the several stations, that even within the narrow confines of Chesapeake Bay, this species is not generally distributed along the shores, but occurs only here and there in closely limited areas, the largest of which is perhaps less than 100^{m} long. This extreme localization within its range is due solely to the requirements of its habitat. The chief conditions necessary for its success are the following:

a) It is limited to tidal beaches, which fact restricts it to a narrow zone, never more than a few meters wide along the shore

b) It requires fresh water, never occurring in water of more than slight salinity. South of Spesutie Island the rivers have a

[10] DRUDE, O., Handbuch der Pflanzengeographie 125. Stuttgart: J. Engelhorn. 1890.

[11] An initial species is called an autochthon and *autochthon* endemism might be used in contradistinction to *relict* endemism. Drude (*op. cit.* p. 124) refers to such species as "vicarious or corresponding forms," from which initial endemism is sometimes called *vicarious* endemism, but the significance of vicarious in this connection is too obscure to commend its adoption.

section near their mouths too salt for the growth of Isoetes, and this salt water section of the rivers becomes longer as we proceed toward the mouth of the bay. This isolates the suitable habitats in one river from those in neighboring rivers.

c) There must be sufficient stability of the soil of the shore to resist the action of the waves, and at the same time sufficient fineness of the soil particles to supply the needs of the plant without requiring an extensive root system. With one exception all the colonies visited by me grew on beaches characterized by rather coarse gravel set firmly in a matrix of sand, and covered over with a thin film of mud. The exception was found at my upper station on Gunpowder River, where a small but unusually luxuriant colony grew in a bed of sand. In this place the shore was protected from severe wave action by a zone of *Zizania aquatica* L., and I have no doubt that this circumstance alone made it possible for Isoetes to retain its hold at this place.

In Engelmann's manuscript notes, the following statement is accredited to William M. Canby: "I don't find any Isoetes (*riparia*, *Engelmanni*, *valida*, or *saccharata*) in pure mud or pure gravel; they always grow in mud which is deposited on gravel beds either by the tides (*riparia* and *saccharata*) or by rains which wash it down (*Engelmanni* and *valida*)."

d) *Isoetes saccharata* also requires that competition with other plants be slight. It is never found forming colonies of such density that it crowds itself, and its most frequent companion species have the same scattered habit. Only at my lower station on Gunpowder River have I found an exception to this. Here it is in competition with *Scirpus americanus* Pers. and is evidently suffering in the conflict. It would no doubt be entirely excluded by the Scirpus if the latter were as robust and densely set as is usual for that species on fresh water beaches.

When we consider the number of apparently essential elements in its habitat and the fewness and smallness of the areas in which all these elements are present, it is easy to understand the extreme localization of the species. But every restriction of habitat increases the difficulty of successful dispersal, and we may well ask how the species has succeeded in finding the places, often

so widely separated, which are adapted to its successful growth. Not only are difficulties presented by the requirements of its habitat, but there are factors in the life-history of *Isoetes saccharata* which are not favorable to rapid dissemination over wide areas. Heterospory is one of these. If spores are carried by any agency, microspores and megaspores must be lodged at the same place or the sporophyte itself must be carried. Besides, there seems to be a tendency in the species to dioecism,[12] and in proportion as this tendency is manifest the difficulties of dispersal are increased.

The means of dispersal upon which this and other species of like habitat may depend are several. The most important means must always be the water currents, because these are always acting at the time and place of spore production. Moreover, the chances are very good that the spores so carried may be lodged along some shore line where a new colony may be formed. In times of storm the waves may tear up whole plants from their anchorage in the littoral gravel and carry them far away to leave them finally stranded on some beach which may be adapted to the growth of the spores thus transported. Late last summer the writer saw a thrifty specimen of *Isoetes saccharata* floating in Chesapeake Bay, 100^{m} east of Stump's Point, at the mouth of Furnace Creek at the head of the bay, over 3^{km} from the nearest known station for the species, though possibly much nearer to some unknown station.

It is conceivable that biotic agencies might also occasionally serve as means of dispersal. Especially, from the observations of Charles Darwin and others, we might expect birds which frequent the shores to carry the spores occasionally on their feet or on their beaks, and as they move from one shore line to another, the spores so carried would be left in a new place favorable to growth. A. A. Eaton (*in litt.*) tells me that ducks are exceedingly fond of the spores of Isoetes, and that the lamellae of their beaks are especially fitted to retain them until washed

[12] PALMER, T. C., 1896, *loc. cit.* A. A. Eaton looks upon dioecism in this species as of rare occurrence, in which case it would be of slight importance in this connection.

out in another locality, and he thinks that this has been perhaps the efficient means of their dispersal.

A third possible method of dispersal is transportation of spores by the wind, but it is evident that successful dispersal by this means must be very rare. In the first place, the wind could only secure spores to carry after they had been stranded on the shore at high tide or in times of storm. Besides, the winds almost invariably blow across the shore line instead of parallel with it, so that the likelihood of the spores being stranded in a place adapted to their development is very slight indeed.

As the distribution of *Isoetes saccharata* appears to be limited by the confines of Chesapeake Bay, while the agency of birds and of the wind are not so limited, these agencies must be assumed to be relatively inefficient. For, if the waterfowl provided efficient means of dispersal, we should expect to find the species following the chief lines of migration as far as there were suitable habitats for its growth. As these lines of migration run parallel with the Atlantic coast, this would specially favor the transportation of *I. saccharata* into Delaware Bay and of *I. riparia* Engelm. into Chesapeake Bay. Our failure to find evidence of any such transportation is peculiarly striking when we bear in mind that the Back Creek station for *I. saccharata* is but little more than 16[km] distant from the nearest point on Delaware Bay, while the known stations on Chesapeake Bay are in some instances separated by distances of more than 80[km].

We must conclude from these facts,[13] I think, that water currents supply the only efficient means of dispersal for this species, and that these have supplied the means by which new colonies have sprung up in more or less distant areas. But even water currents could scarce be adequate to carry the spores from one

[13] This entire discussion is based on the assumption that *Isoetes saccharata* and *I. riparia* are really distinct species, as they have always been considered. In some of its forms *I. saccharata* approaches so nearly to *I. riparia* that the suggestion is not far that they are ecological varieties of the same species. Too little is known, as yet, about ecological varieties, to make more than a suggestion permissible. It is obvious that successful transportation from the one bay to the other may have taken place any number of times, if in each case the ecological conditions were such as to produce from the spores of a single specimen, *I. riparia* in Delaware Bay and *I saccharata* in Chesapeake Bay.

station to the mouth of the river in which it occurs, thence up or down the coast to a neighboring river, and up that river to the fresh-water portion near the head of tide water. Such a transportation, if at all possible, must depend upon the most exceptional of circumstances.

Probably a truer explanation is found in relation to the geological history of the bay. It is believed by some geologists[14] that the region about Chesapeake Bay is now sinking, and it is certain that it has recently sunk after a period of elevation. In fact, it seems to have been elevated and depressed several times in its Pleistocene history.[15]

The position of old shore lines with their sea cliffs and terraces gives evidence of the amount of subsidence of the land at each period of sinking, but no evidences remain as to the height to which the land rose during each period of elevation. The present elevation of the land is such that the water of the bay is fresh to Spesutie Island, about ten kilometers below the mouth of the Susquehanna River. During periods of greater elevation the water was fresh further to the south. When the land was so elevated that the water was fresh at the mouth of the Potomac River, favorable habitats along the shore of the bay must have been occupied by the progenitors of the *Isoetes saccharata* colonies which now occur in the upper estuarine portion of the tributary rivers. As the land sank and the rivers were ponded farther and farther from their mouths, new areas became adapted to the growth of Isoetes, and new colonies were formed. Simultaneously the colonies furthest down stream were destroyed by the advance of salt water. In this way there came to be, instead of a single colony or group of colonies at the head of Chesapeake Bay, as many distinct colonies as there were ponded tributaries. So long as the land continued to sink, the successful reproduction was on the up-stream side, and destruction followed *pari passu* on the down-stream side until the present condition of widely separated colonies was brought about. In periods of

[14] Cook, George H., Geology of N. J. **1868**: 343 *et seq.*

[15] McGee, W J, Am. Jour. Sci. **35**: 463–466. 1888. Darton, N. H., Bull. Geol. Soc. Am. **2**: 450. Ap 1891. Shattuck, George B., Am. Geol. **28**: 100–105. Ag 1901.

elevation, the reverse process must have taken place, and the many distinct areas must have been merged again into one. This may have taken place as often as the bay has been up and down, and certainly has happened as often as the bay has risen and fallen since *Isoetes saccharata* entered it.

Just how or when Isoetes entered Chesapeake Bay is, of course, impossible to say, except that, according to this hypothesis of its dispersal, it must have been introduced before the last sinking of the coastal plain.

From what has been said of the requirements of its habitat and the means of dispersal of Isoetes, it will be seen that the barriers between Chesapeake Bay and Delaware Bay and between both of these and other fresh tidal waters, are of such definite character as to render these bays virtually islands of water in oceans of land. As we find *Isoetes saccharata* nowhere else than in Chesapeake Bay and *Isoetes riparia* nowhere else than in Delaware Bay, it seems fair to assume that neither of these species ever existed as such outside of the body of water to which it is now limited, and that we have here examples of initial endemism entirely comparable with that so common upon oceanic islands.

These two species are closely related and probably stand to each other in relation of parent and offspring; but which is the parent and which the offspring may not be easy to decide. Or perhaps they were the offspring of a common parent different from both. The nearness of this relationship was emphasized in the recognition of the two varieties, *Isoetes saccharata Palmeri* A. A. Eaton and *I. saccharata reticulata* A. A. Eaton, both possessing characters intermediate between *Isoetes saccharata* Engelm. and *Isoetes riparia* Engelm. The significance of these forms will be increased rather than lessened if they should prove to be untenable as varieties. For if these varieties are shown to be simply stages in the development of a polymorphic species, the greater range of variability which must then be admitted as a character of *I. saccharata* Engelm., coupled with the fact that those variations in several different features are in the direction of *Isoetes riparia* Engelm., would make almost certain the inference that an extreme variation of *I. saccharata* had become somewhat fixed through its isolation in Delaware Bay.

Careful cultures will be necessary to demonstrate conclusively the polymorphism of *Isoetes saccharata* Engelm., but that seems at present the most satisfactory explanation of the following facts. My attention was called both by A. A. Eaton and T. C. Palmer to several futile attempts which had been made to secure *typical* material from the *type* locality. It appears that the original description was written from a form which is of very rare occurrence. Even the co-type material did not agree with the type, and the Wicomico station has been visited several times since, but no typical material has been secured there. The infrequency of the recurrence of the typical form is well shown by the fact that my collection from Hunting Creek, Va., appears to be the first material collected since 1863, which agrees in its spore characters with the type material. The striking fact here is that my collection of typical *I. saccharata* Engelm. came from the type locality of variety *reticulata* A. A. Eaton. This colony is only a few square meters in extent and a considerable number of specimens had been collected there by Vasey and Coville in 1888, and by W. R. Maxon in 1900 and 1901. Every one of those specimens appear to have been var. *reticulata*. I collected at the same place perhaps a dozen specimens, every one of which was typical *I. saccharata*. The only plausible explanation of these facts, it seems to me, is that the identical plants which had been var. *reticulata* at the time of the previous collections, were last year typical *I. saccharata*.

Another similar circumstance which lends support to this explanation is that E. S. Steele's collection at Four Mile Run in 1899 was nearly typical *I. saccharata*, whereas the considerable number of specimens secured by me in 1902 from the same spot, all showed extremely well-marked characters of var. *reticulata* A. A. Eaton.

I have no such striking facts against the validity of var. *Palmeri* A. A. Eaton, since I visited no *Palmeri* station, but much of my material from the head of the bay was intermediate between *I. saccharata* and var. *Palmeri*, as was also Coville's Mount Vernon collection. T. C. Palmer found the same conditions at Cabin Johns Creek and Town Point in Elk River. If

Isoetes saccharata should prove to be polymorphic, as these facts suggest, the result will be of interest in its bearing upon such species as *I. echinospora* Durieu and *I. velata* A. Br., whose numerous intergrading forms have proved so baffling to systematists.

By way of summary, then, *Isoetes saccharata* Engelm. has been located in a number of tributaries of Chesapeake Bay from the the Potomac and Wicomico Rivers to the head of the bay.

The species is conceived to be autochthonous in Chesapeake Bay, and to bear toward *Isoetes riparia* Engelm. the relation of parent to offspring.

Its present distribution is explained by the geomorphic movements of the coastal plain.

Certain facts are presented which suggest that the species is polymorphic, and that the varieties *Palmeri* A. A. Eaton and *reticulata* A. A. Eaton are untenable.

I take pleasure in acknowledging my indebtedness to Wm. M. Canby, F. V. Coville, T. C. Palmer, E. S. Steele, and W. R. Maxon for notes on their several collections of *Isoetes saccharata* Engelm. and its forms; to Dr. J. N. Rose for data from U. S. National Herbarium, and Dr. Wm. Trelease for data from the Herbarium of the Missouri Botanical Gardens, and from G. Engelmann's manuscript notes; also to Miss Veva M. Brower for notes on the Nanticoke River at Seaford, Del. But I am under special obligations to A. A. Eaton, who has kindly examined all my material and has encouraged me with suggestions and criticisms on the discussions involved in this paper. To all of these I wish to express my sincere thanks.

THE UNIVERSITY OF CHICAGO.

A SKETCH OF THE FLORA OF SOUTHERN CALIFORNIA.

S. B. PARISH.

THE name "Southern California" is here restricted to a territory somewhat less extensive than that to which it is sometimes applied; but even as here limited, to the five southernmost counties—Los Angeles, San Bernardino, Riverside, Orange, and San Diego—it includes one quarter of the area of the whole state, and exceeds in size the great state of Ohio. It has an area of 40,889 square miles (over 100,000 sq. kilometers). Its greatest breadth, from north to south, is 210 miles (336 km), and from east to west 282 miles (451 km). It lies between 32° 30′ and 35° 40′ north latitude, and between 37° 15′ and 42° longitude west from the meridian of Washington. Its western boundary is formed, for the greater part, by the Pacific Ocean, but partly by the counties of Ventura and Kern, and these two counties, together with Inyo, bound it on the north, while for a short distance on the northeast it touches the state of Nevada. The river Colorado separates it on the east from Arizona, and on the south it adjoins the Mexican state of Lower California.

Before proceeding to a consideration of the flora of this region it is desirable to speak briefly of the physical character of its surface, and of its climate, since these are the most important influences by which the development and distribution of its plant population have been determined.

OROGRAPHICAL FEATURES.

The region is one of mountains, whose ramifications embrace numerous valleys of greater or less extent. The main axis of upheaval is a continuation of the Sierra Nevada. It enters our region at Ft. Tejon, in which neighborhood the Coast Range unites with it; and it extends in a course from northeast to southwest, culminating in the twin summits of San Bernardino and Grayback, respectively 10,100 ft (3,080 m) and 11,725 ft

(3,575 m) above sea level. The mountains between these limits are generally called the San Bernardino Range.[1] It is made up of the Sierra Liebre and Sierra Pelona, between Tejon and Soledad Passes; the San Gabriel Mountains, with the peaks of San Gabriel, 6,232 ft (1,900 m), San Antonio, 10,120 ft (3,085 m), and Cucamonga,[2] 6,500 ft (1,980 m), between Soledad and Cajon Passes; and the San Bernardino Mountains proper, between Cajon and San Gorgonio Passes.

North of Soledad Pass the mountains are comparatively low, but rugged and broken. An important cross range, the Santa Monica, maintaining an altitude of 2,000 to 3,000 ft (600–900 m), stretches from San Fernando Peak, 3,793 ft (1,156 m), to the Pacific Ocean at Point Duma. But south of Soledad the mountains become higher, towering up abruptly, from a valley base 500 to 1,000 ft (150–300 m) above the sea, to a ridge line having an altitude of 5,000 to 6,000 ft (1,500–1,800 m). From the desert they present a less lofty appearance, since on that side the base altitude is 3,000 to 3,500 ft (900–1,066 m).

Grayback throws out an important spur, in the direction of the main range, towards the Colorado River. This may be known as the Chuckawalla Range, although that name is often restricted to its further extremity. It separates the Colorado and the Mojave[3] Deserts.

The low San Gorgonio Pass separates Grayback from San Jacinto Mountain 10,805 ft (3,993 m), an air-line distance of some twenty miles. The mountains here spread out, their course changes, and is less defined. But regarding the line which divides the watershed draining into the Pacific from that which drains into the desert, its direction is found to be about 10°

[1] First by Blake in Pac. R. R. Rep. 5. He also suggested the name "Peninsular Range" for the mountains extending from San Jacinto into Lower California, but this name, although appropriate, has failed to find acceptance.

[2] This was a troublesome name to the early explorers. It is Quiqual Gungo of Pac. R. R. Rep. 4: 38; Quiquai-mungo *ibid.* 5[2]: 80; and Kikal Mungo *ibid.* 7: 8.

[3] I use the spelling long current in California. While only the Spanish orthography of an aboriginal name, it harmonizes with such Spanish names of the region as Tejon, Cajon, etc. The U. S. Board on Geographical Names has adopted the form "Mohave," but this should not be allowed to supersede a well-established local usage. The name was first printed by Fremont in 1844, who spelled it "Mohahve."

south of east. Here it is the desert face which is precipitous, its base, for the most part, not exceeding 500 ft (150 m) above sea level, while upon the other side San Jacinto overlooks a confusion of ridges and lesser peaks.

A main cross-range from San Jacinto parallels the San Bernardino Mountains at a distance of about forty miles. It comprises the Palomar Mountains[4] (summit 5,800 ft, 1,765 m) and the Temescal Mountains, whose terminal summit, Santiago Peak,[5] has an altitude of 5,675 ft (1730 m), and separates the San Jacinto Valley from the coast region.

Further south Cuyamaca Mountain, 6,500 ft (1,980 m) high, dominates a rugged region of high ridges and narrow valleys. In default of a better name the entire chain, from Tejon Pass to Cuyamaca, may be called the Nevadan Range, since it is, in truth, a part or a continuation of the Sierra Nevada.

THE DESERTS.

The topography of the desert region is less accurately known. It comprises two distinct divisions: the Colorado Desert and the Mojave Desert. The former, stretching southeastward from San Gorgonio Pass to the Mexican boundary, is a great valley, 180 miles (288 km) long, and 30 to 50 miles (50–80 km) wide. In its center it sinks into a deep depression over 250 ft (76 m) below sea level,[6] the dry bed of what has been in prehistoric times first an arm of the sea, and later a fresh or brackish lake. In this depressed area, and notably near Salton, volcanic forces yet manifest themselves in "mud volcanoes" and extensive solfataras.

The lower part of this desert, toward Yuma, and in the New River region, consists largely of pebble-covered clay plains and

[4] Also known as Smith Mountains.

[5] Sometimes called Saddleback, or Santa Ana peak. In 1861 Dr. Whitney gave it the name Mt. Downey, which fortunately has never been accepted. This whole range is often called the Coast Range, but it has no connection with the true Coast Range of California.

[6] The following are the altitudes in feet at stations on the Southern Pacific Railway where it crosses this depression: Seven Palms, 582; Indio, −20; Walters, −195; Dos Palmas, −253; Salton, −263; Flowing Well, 5; Tortuga, 185. The total distance, in a straight line, is about 80 miles (130 km).

shifting sand hills, and has an altitude of 150 to 400 ft (45–120 m). The area of the Colorado Desert has been estimated at 9,000 square miles (14,400 sq km).[7]

The Mojave Desert lies on the north side of the San Bernardino Range, and its continuing spur, the Chuckawalla Mountains; eastward it stretches to the Colorado River, and northerly to and beyond our boundary lines. Its greatest length, east and west, measured in an air-line, from Gormans Station, at the head of Antelope Valley, to the Needles on the Colorado River, is about 130 miles (210 km). Its width, north and south, from the mountains which form its southern rim to our northern boundary, varies from 30 to 60 miles (48–96 km). No estimate of its area appears to have been made. Within our limits its altitude is much greater than that of the Colorado Desert, being 2,000 to 3,500 ft (660–1,067 m), but beyond them it also sinks, in Death Valley, below sea level.

Its whole surface is cut up by short isolated ranges and "lone mountains," which are surrounded by sloping mesas, or enclose basins whose lowest portions are occupied by "dry lakes." Some of these are level expanses of hard, elastic clay, smooth and bare as a racetrack, and bordered by a narrow belt of nitrophilous vegetation. Receiving the scanty storm water that rolls down from the bare hills about them, they at times may be transformed into tenacious mud, or even be covered by a few inches of water. Or the floor of these basins may consist of what prospectors call "self-rising soil," a deep bed of loose alkaline powder, slightly crusted over, into which foot and wheel sink wearily; or, again, it may be covered with a snowy incrustation of soda salts.

The highest mountain of the Mojave Desert is Ivawatch, 6,290 ft (1,917 m), on the northern boundary of San Bernardino county. Some twenty miles southwest is Pilot Knob, 5,525 ft (1,684 m), a noted landmark, as its name indicates. Mt. Manchester, near the Needles, is 4,570 ft (1,448 m) high. But the most important of these ranges are the Providence Mountains,

[7] This is for the part of it within the United States; beyond the boundary it continues to the Colorado River and the head of the Gulf of California. Its width on the Colorado River is fully 75 miles (120 km).

situated on the eastern border of the desert, and extending some 75 miles (120 km) in a NNE and SSW course, culminating at the south in Mt. Edgar, 6,350 ft (1,935 m).

DRAINAGE SYSTEMS.

A country such as I have described, if in a region of abundant rainfall, would abound in limpid lakes, and in living streams, some of which would be of considerable volume. But far other is the case under the arid conditions which here exist. Even the streams rising in the high mountains of the San Bernardino range are infrequent, slender and inconstant; and of still less importance are those which drain the mountains to the south. In seasons of unusual precipitation they become raging torrents, and at such times the larger streams may carry their waters to the sea; but ordinarily their volume is insufficient to reach their nominal mouths, while in summer they dwindle down to thin rivulets which repeatedly sink and reappear in their wide sandy beds.

The San Gabriel Mountains give rise on their desert slopes to Rock Creek,[8] which ventures beyond their base only in wet weather. On their seaward side they are drained on the west by the Los Angeles and San Gabriel Rivers, and on the east by Lytle Creek, a tributary of the Santa Ana.

The San Bernardino Mountains furnish the waters of the most important streams of the whole region. On the northern watershed the Mojave River has its source in Holcomb Valley, at an altitude of 7,000 ft (2,134 m). It flows 75 miles (120 km) in a northerly direction, and then turning to the east continues for 60 miles (96 km) further, the distances being measured in an air line, but following its meanderings its length is fully 200 miles (320 km). In its course it disappears eight times in its sandy channel, leaving it entirely dry for long intervals, and is finally lost in Soda Lake (alt. 1,116 ft, 340 km), a flat, elliptical depression some 70 square miles (112 sq km) in area, occasionally flooded a few inches deep with water, but usually whitened with alkaline efflorescences. The eastern drainage of these mountains forms

[8] This is the "Johnson's River," of Blake, Pac. R. R. Rep. 5:30 *et seq.*

the Arroyo Blanco, or Whitewater, a strong stream which is soon lost in the sands of the Colorado Desert.

The Santa Ana River carries the seaward drainage, and has an airline course of 85 miles (136 km), in a southwest direction, to the ocean, which, it is said, its waters have been known to reach in high floods. In ordinary stages it sinks soon after disemboguing from the mountains, and reappearing after ten miles (16 km) carries more or less water nearly to Santa Ana.

San Jacinto Mountain gives rise to a stream bearing the same name, which follows a southwest course to Elsinore Lake. Its channel, however, is only intermittently supplied with surface water. The Santa Margarita, the San Luis Rey, the Sweetwater, and some lesser streams, drain the mountains of San Diego county, and have a character similar to those already described.

The Colorado River, which touches the border of the state, does not receive from it a single tributary, great or small; but an abandoned channel, the so-called New River, carries the waters of the Colorado, in times of great floods, into the southeastern part of the desert and to the Salton Sea.

GEOLOGICAL FORMATIONS.

The great mountain axis consists principally of granitic formations, and such is the prevailing character of the subordinate ranges. There are occasional outcroppings of limestones, but always of limited area. A range of Tertiary hills, conglomerates, sandstones and shales, beginning near Pasadena, stretches to the Santa Ana River, where it is divided by the granites of the Temescal Mountains, a narrow arm continuing along their northeastern base, while a wider one (10–18 miles, 16–29 km) turns toward the coast, which it reaches at San Juan, and follows it thence to the Mexican boundary. A less important Tertiary formation skirts the southern base of the San Bernardino Mountains from Santa Ana Cañon to the Whitewater, occupying an area of 30 miles (48 km) in length by 1 to 5 miles (1.6–8 km) in width. The same formation also appears in the Palos Verdes hills, and on the islands off the coast.

The San Fernando Plains, the wide expanse of fertile country

between Los Angeles and Santa Ana, the San Bernardino, San Jacinto, and many smaller valleys are Quaternary and Recent. They include sandy and gravelly mesas, as well as rich loams, ferruginous clays, and black adobe. Almost without exception they contain soda salts, from the small percentage which increases fertility, to the excess which forbids the growth of all but a few specialized plants. Recent formations also prevail throughout the Colorado Desert.

The formations of the Mojave Desert are less well known. The mountains are, for the most part, granitic, the intervening mesas and valleys being of recent deposition. Evidences of former volcanic activity are exhibited in places. This is most marked in the country between Point of Rocks and Bagdad, on the Santa Fé Railway, an air-line distance of some 80 miles (130 km). Here the rocks are metamorphosed, and often display commingled bands and patches of reds, blues, greens, purples and yellows.[9] The mesas are strewn with scoria, the hills have black lava caps, fissure lines are seen, and lava streams may be traced for miles. Not less than a dozen volcanic cones are known in this region. One of the largest is 450 ft (137 m) high and 3,000 ft (914 m) in diameter at base; the extinct crater at the summit is 750 ft (228 m) in diameter and 150 ft (45 m) deep. The Providence Mountains limit this volcanic area on the east, but northward other less known centers exist.

CLIMATIC CHARACTERISTICS.

Southern California possesses a variety of climates, but throughout the larger part of it aridity and high temperature are the dominant features. There are few, if any, absolutely frostless localities, but there are many where only light frosts ever occur, and which may be quite untouched for several successive years. At altitudes below 1,500 ft (457 m) the midwinter temperature rarely falls below 25° F. (−4° C.), and the same altitude marks the ordinary limit of even light snowfalls.

But ascending to higher altitudes a different climate and a cooler temperature is soon reached. Thus at San Bernardino

[9] This peculiar coloration gave the Calico Mountains their prosaic name, in reference to their variegated tints.

(1,075 ft, 328 m) in the five years 1895–9 the highest point reached by the thermometer was 110° F. (43° C.) and the lowest 23° F. (−5° C.).[10] At Little Bear Valley, 5,150 ft (1,569 m), in the adjacent mountains, distant about 12 miles (20 km) in an air line, the extremes during the same years were 93° and −2° F. (34 and −19 C.).[10a] That is, a temperature was reached in summer in the valley 17° above that of the mountain, while the winter temperature lacked 21° of falling so low. At Big Bear Valley, 6,500 ft (1,981 m) a temperature of −14° F. (−25.5° C.) has been observed,[11] frosts occur in midsummer, and ice sometimes forms on an August night. No observations have been made at greater altitudes, but it is evident that at 10,000 or 12,000 ft (3,000–3,600 m) very low temperatures must be reached. These lofty summits are white in the winter months, and on their northern slopes the snow fields often linger late into summer. After a winter of unusual accumulations some shrunken remains may even persist into a second season.[12] Even at altitudes as low as 6,000–7,000 ft (1,830–2,130 m) there are sheltered cañons where snow banks yet linger at midsummer.

Contrary to common opinion, recorded observations establish the fact that lower temperatures are reached at stations in the desert region than at places having the same altitude on the seaward side of the mountains.[13] A great difference is shown also at the other extremity of the scale. The highest temperatures recorded on the coast are 85°–100° F. (30–38° C.); further back from the sea 100°–112° F. (38–44° C.) is reached; but at stations in the deserts records of 115°–128° F. (46–53° C.) have been made.[14]

The annual precipitation is very unequal in amount, not only in the different regions, but in the same region in different years. As an example of yearly variability the rainfall at Los Angeles

[10] From the Records of Dr. A. K. Johnson.

[10a] Records of Arrowhead Reservoir Co. [11] Records of the Bear Valley Co.

[12] Mean annual snowfall at Little Bear Valley 1895–9, 73 in (1,854 mm); greatest single snowfall, 39 in (990 mm). Records of Arrowhead Reservoir Co.

[13] At Victor, in the Mojave Desert, altitude 2,713 ft (828 m) killing frosts occur in August.

[14] At Mammoth Tank, July, 1887, 128° F.; July, 1884, 126° F.

of 32.25 in (819 mm) in 1869 may be compared with that of 4.83 in (122 mm) in 1898. In the desert region the rainfall is always very small, and in average seasons is greatly exceeded by that of the cismontane region, but years of extreme drought have occurred in which the difference was less marked.

The appended table exhibits the normal amount of precipitation at places whose records extend over a period of more than fifteen years. The average for the three intramontane stations is 14.95 in (380 mm), or about five times that of the desert station.

NORMAL PRECIPITATION.

Stations	Altitude		Years of Record	Monthly Precipitation				Yearly Precipitation	
				Least		Greatest			
	Feet	Meters		In.	Mm.	In.	Mm.	In.	Mm.
Los Angeles	270	84.1	21	T	T	4.0	102	18.1	460
San Diego	12	3.6	42	0.1	2.5	2.1	53	9.8	249
San Bernardino	1,075	327.6	29	0.3	7.6	3.6	91	17.0	432
Yuma	140	42.7	16	T	T	0.6	15	3.2	77

Nearly as great a disparity exists between the rainfall of the intramontane and the Nevadan regions, but data from the latter are few and not easily obtained. A partial means of comparison is afforded by the following table. The seasons are from July to June. The distance of the two stations in an air-line is about 12 miles (20 km); the difference of altitude is 4,075 ft (1,242 m).

PRECIPITATION FOR SIX SEASONS, 1893–94 TO 1898–99.

Stations	Altitude		Precipitation					
			Greatest		Least		Mean	
	Feet	Meters	In.	Mm.	In.	Mm.	In.	Mm.
San Bernardino[14]	1,075	328	20.98	533	7.49	190	11.61	295
Little Bear Valley[15]	5,150	1,570	60.61	1,542	19.79	502	33.08	840

The rainfall at the mountain station is nearly three times

[14] Dr. A. K. Johnson's record. [15] Arrowhead Reservoir Co.'s record.

that of the subjacent valley. The seasons of greatest and least rainfall were synchronous.

But for the purposes of the present inquiry the extreme of moisture and drought to which plant life is exposed is of as great importance as the average amount of rainfall; and the distribution in time of this amount is a factor of equal value. Again it will be found that in these respects the desert vegetation is at a disadvantage. Throughout the deserts total yearly rainfalls of 1.5 to 4 in (38–101 mm) are the rule, and at some stations a whole year may pass with absolutely no measurable precipitation. But this small amount is so evenly distributed through the year as to produce much less effect, certainly for annual plants, than if it were concentrated in a few months. The table below shows the normal distribution of rainfall throughout the year at two desert stations, compared with that at two stations on the coast.

NORMAL MONTHLY PRECIPITATION IN INCHES.

Stations	Years	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Keeler	8	0.2	0.4	0.2	0.3	0.4	0.2	0.1	0.2	0.3	0.3	0.4	0.4	3.3
Yuma	16	0.4	0.6	0.2	0.1	T	T	0.1	0.4	0.1	0.3	0.3	0.6	3.2
San Diego	42	1.6	2.1	1.0	1.0	0.3	0.1	0.1	0.1	0.1	0.3	1.0	2.1	9.8
Los Angeles	21	3.9	4.0	2.2	1.3	0.3	0.1	T	0.1	T	0.7	1.6	3.7	18.1

It here appears that the scanty rainfall of the desert stations is quite evenly distributed through the whole year, while at San Diego 9.1 inches out of the total 9.8 inches, and at Los Angeles 17 inches out of 18.1 inches fell during the growing season between November and May. That is, over 95 per cent. of the total rainfall at these places comes at a time when, owing to a lower temperature and a more declined sun, it is not subject to rapid evaporation, and avails most for the growth of vegetation. On the other hand almost all the desert rainfall may be regarded as ineffective by reason of its equal distribution.

It must be remembered, however, that all our recorded observations were made at stations in the open deserts, whereas had they been made in the cañons of the circumscribing mountains, somewhat more favorable results would have been obtained.

The rainclouds hug the mountains, and in winter one often may pass from the bright sunshine of the desert valleys through mist and drizzle to heavy showers by ascending for a few miles some cañon leading up the mountains. Hence it is in the cañons that the botanist learns to expect the most abundant and varied vegetation.

The desert mountains are also the scenes in midsummer of "cloud-bursts," or violent thunderstorms. These discharge in a short period and over a limited area a great quantity of water, and for a few hours the parched cañons are filled with rushing torrents. I have found a measurement of but one of these "cloud-bursts," and that only partial. At Campo on a day in August, 1891, there fell in such a storm 16 in (406 mm) of rain, before the gauge was washed away, preventing a complete measurement.

On the seacoast the aridity of the atmosphere is modified by frequent fogs and damp air-currents from the sea; and these ameliorating influences extend their benefits, in a less degree, inland, but do not pass beyond the mountains to modify the dryness of the desert air, while the strong winds almost constantly blowing there, produce a further desiccating effect.

PHYTOGEOGRAPHICAL AREAS.

It will readily be understood, from the preceding account, that the region under consideration consists of three divisions, differing from one another in both topography and climate. Consequently each of these will be found to possess a distinct and characteristic flora, and to constitute a separate life area.

In its relation to the biological divisions proposed by Dr. Merriam[16] the entire territory may be regarded as a part of the Sonoran province, in the midst of which arise two isolated peaks belonging to the Boreal province. A scanty Arctic flora occupies the summits of these peaks, and beneath it a diligent study can disentangle the Hudsonian and Canadian zones. This has been worked out very carefully and thoroughly by Mr. H. M. Hall,[17]

[16] MERRIAM, J. HART, N. Am. Fauna 3:20, map 5; National Geo. Mag. 6:229; Yearbook U. S. Dept. Agr. **1897**:203.

[17] HALL, HARVEY M., A botanical survey of San Jacinto Mountain. Univ. of Cal. Pub. Bot. **1**:1–144.

THE VERMONT BOTANICAL CLUB held its ninth annual field meeting at Arlington and Manchester in southern Vermont on July 3 and 4. There was a good attendance, including visiting botanists from Minnesota, New York, Massachusetts, and New Hampshire. The weather was ideal and the ascent of Mt. Equinox, under the guidance of Judge and Mrs. Loveland Munson, was a delightful mountain climb which afforded much of botanical interest. This club now has about one hundred and sixty active members.

DR. H. G. TIMBERLAKE, assistant professor of botany in the University of Wisconsin, died suddenly on July 19 at the age of thirty. He was taking a bath and seems to have slipped on the curved bottom of the enameled tub and fallen over the side, striking his head violently on the floor and rupturing a cerebral artery. Death occurred before a physician could reach him. Dr. Timberlake had recently been promoted to an assistant professorship and was married on June 30 to Miss Violet Slack, an assistant in the department.

THE COMMITTEE OF ORGANIZATION for the International Botanical Congress at Vienna plans to have the meetings on June 13–18, 1905, giving the mornings to addresses and discussions of topics of present importance (a morning to some one subject), and the afternoons to the nomenclature problem. The morning of the fifteenth will be reserved for a meeting of the Association internationale des botanistes. A great botanical exposition is planned, at the time of the Congress, in the palace at Schönbrunn; and excursions, botanic and scenic, before and after the Congress, will be arranged.

IT IS PROPOSED to organize a society for horticultural science, the object of which shall be more fully to establish horticulture on a scientific basis. The membership will naturally be made up of the horticulturists of the experiment stations and of the U. S. Department of Agriculture, together with other scientific men whose work has a horticultural bearing. The meetings will be held in connection with those of some kindred society, as the American Pomological Society or the American Association for the Advancement of Science. Any botanists interested are requested to address S. A. Beach, Horticulturist, New York Agricultural Experiment Station.

WITH THE TENTH VOLUME the *Annuario del Real Istituto Botanico di Roma*, founded by Professor R. Pirotta in 1884, comes to an end. In its place there is to appear the *Annali di Botanica*, which will be published in small fascicles in order to avoid the long delay of a more voluminous journal. The new publication will include not only original researches in all fields of botany, but also analytical reviews of important papers and synthetical reviews of current questions. Particular attention will be given to the history of botany in Italy and to making known all facts regarding the Italian flora. The first fascicle was published on May 15, and the second on June 30.